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E. J. Denton and D. M. Rowe

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Reflective communication between fish, with special reference to the greater sand eel, *Hyperoplus lanceolatus*

E. J. DENTON[1] AND D. M. ROWE[2]

[1]*Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, U.K.*
[2]*School of Computing, University of Plymouth, Drake Circus, Plymouth PL4 8AA, U.K.*

SUMMARY

The reflecting units in the surfaces of silvery fish are small 'platelets' which have various orientations with respect to the surfaces in which they lie. In the fields of light found in the sea, these orientations are often such as to enable fish to make themselves almost invisible from most points of view. Here we show that the platelets can also be useful in signalling information about the movements that the fish are making. Such signals are clearly graded. Some, e.g. those that accompany C-starts, will be strong and visible at distances many times the length of the fish. Others, e.g. those given by a spot of silveriness on the tail, will only be visible to near neighbours. We consider the movements of fish in terms of three components, rolling, pitching and yawing and show that, by virtue of the organization of the silvery layers, a given movement will produce, to the eye of a neighbour, a characteristic changing pattern of bright and dark surfaces. The changes in brightness accompanying quite small movements are large and, to us and almost certainly to the fish, much more visible than the changes in shape or position (the detection of which must also depend on differences in brightness). Diffusely reflecting surfaces can, to some degree, serve the same purpose but they are less good at doing so. They certainly cannot give a fish the facility of passing quickly from being almost invisible to presenting striking unequivocal signals to their neighbours, as silvery surfaces do.

We give an account of the reflecting surfaces of the greater sand eel, *Hyperoplus lanceolatus* (Le Sauvage), in relation to this hypothesis.

1. INTRODUCTION

It is generally agreed by divers that when silvery fish, like the herring, are swimming quietly they are, from most points of view, difficult to see. In a general way Franz (1907) and Ward (1919) realized that fish could camouflage themselves by reflecting their surroundings. With better knowledge of the properties of submarine light, it became possible to show that in mid-waters good camouflage depends on the patterns and orientations of the reflecting material (see Denton 1970).

It is also common knowledge that when a school of silvery fish is disturbed, e.g. by the attack of a predator, then, as the fish twist and turn, they emit transient bright flashes of light that are confusing to the attacker. Ward also notes that when a fish becomes diseased or weak it sometimes rolls and only rights itself with an effort. Its track is then marked by a series of protracted flashes that attract other fish and he discusses the value of 'flash' in our fishing lures, such as spoons, salmon flies and wet trout flies in the light of this observation. There seems little doubt that, in the sea, some fish use patches of light as lures, simulating the appearance of smaller fish which would have been prey to the fish that are attracted (see, for example, Myrberg 1991). Dr G. W. Potts tells us that he has strong evidence, from his careful and sustained monitoring of the behaviour of fish in the sea in a variety of circumstances at different stages of their lives, that flashing light signals are undoubtedly used by fish (including the pollock and sand eels), e.g. during feeding activities. Vision is so important in the behaviour of most fish that it would, perhaps, be surprising if patterns of light, whether arising from diffuse or specular reflections, or from luminescence, were not used as signals.

In this, and in a subsequent paper dealing with coloured reflectors, we shall argue that, in some fish: (i) the platelets, which are the functional units of the reflective systems, have their flat surfaces at angles which are oriented differently in different regions of the external surfaces, so that when movements of a fish change the angular relations between the fish and the ambient light field, this produces changes in the patterns of brightness over the surface of the fish; (ii) that these changes can give highly informative signals of the nature of the movements to neighbouring fish; and (iii) such communication is made possible by the special properties of submarine daylight and of the reflectors. These properties will be briefly described.

(A brief note on this hypothesis is given in the Report of the Council of the Marine Biological Association of the UK for 1990.)

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(*a*) *Angular distribution of daylight in the sea*

The angular distributions of daylight found in the sea differ markedly from those found on land (for an excellent general account of submarine illumination appropriate to the work described here, see Duntley (1963); ecological aspects are well covered by Lythgoe (1979)). With increasing depth, in a homogeneous water mass, the penetrating daylight progressively approaches an 'asymptotic' radiance distribution with angle. This distribution depends only on the properties of the seawater and not at all on the altitude of the sun, the cloudiness of the sky or waves on the surface (Whitney 1941; Preisendorfer 1959). At shallow depths the radiance peaks approximately in the direction of the refracted rays from the sun. As depth increases the angular distribution becomes less sharply peaked and approaches the final form whereas its maximum moves (more slowly) towards the zenith.

A series of underwater radiance distributions measured by Tyler (1960) in the plane of the sun at progressively greater depths in a deep lake in Idaho are shown in figure 1. Now suppose that a fish in such a light field has its antero-posterior axis horizontal and perpendicular to the vertical plane containing the sun. If its body is oriented so that its back is directed vertically upwards, the fluxes of light falling on, and being reflected by, its left and right sides will at shallower depths be very different from one another. For the data of figure 1, we show in figure 2 the ratio of the radiances of light at equal angles from the vertical. We see that, for example, at a depth of 4.24 m, for an angle of 30° from a downward vertical from the surface of the sea, this ratio is over 100 times. At 29 m, this ratio would still be over six times. Clearly, with the fish oriented 'vertically', one side of the fish would appear very bright, and the other very dark against the backgrounds against which they would be viewed. With the fish oriented this way, silvery sides would make them very visible indeed. However, although the angular distributions of light found at shallow depths are far from being symmetrical about a vertical to the surface, for all depths axes can be found around which the distributions of light are almost symmetrical (see figure 3). An analysis of data on comparable results obtained by Jerlov & Fukuda (1960) on Gullmar Fjord in the Baltic gave closely similar results. Now it is well known that fish commonly turn their backs towards the direction from which the most intense light comes (von Holst 1950). We have, moreover, observed in laboratory experiments that when herring are subjected to oblique light distributions, they tilt their bodies so as to equalize the light fluxes falling on their left and right sides. When exposed to changing light fields, e.g. when swimming round a tank with oblique lighting, herring change their orientation very quickly so as to adapt to the changing light distributions to which they are successively exposed. In these conditions, herring will tilt their bodies through very considerable angles (greater than 40°) in directions that would approximately equalize the light falling on their left and right sides as they move between different light fields. We may note that this problem will not exist on cloudy days, nor on sunny days for fish facing either directly away from or towards the direction of the sun, and can be evaded by the fish avoiding the surface waters on sunny days. We shall assume that when a

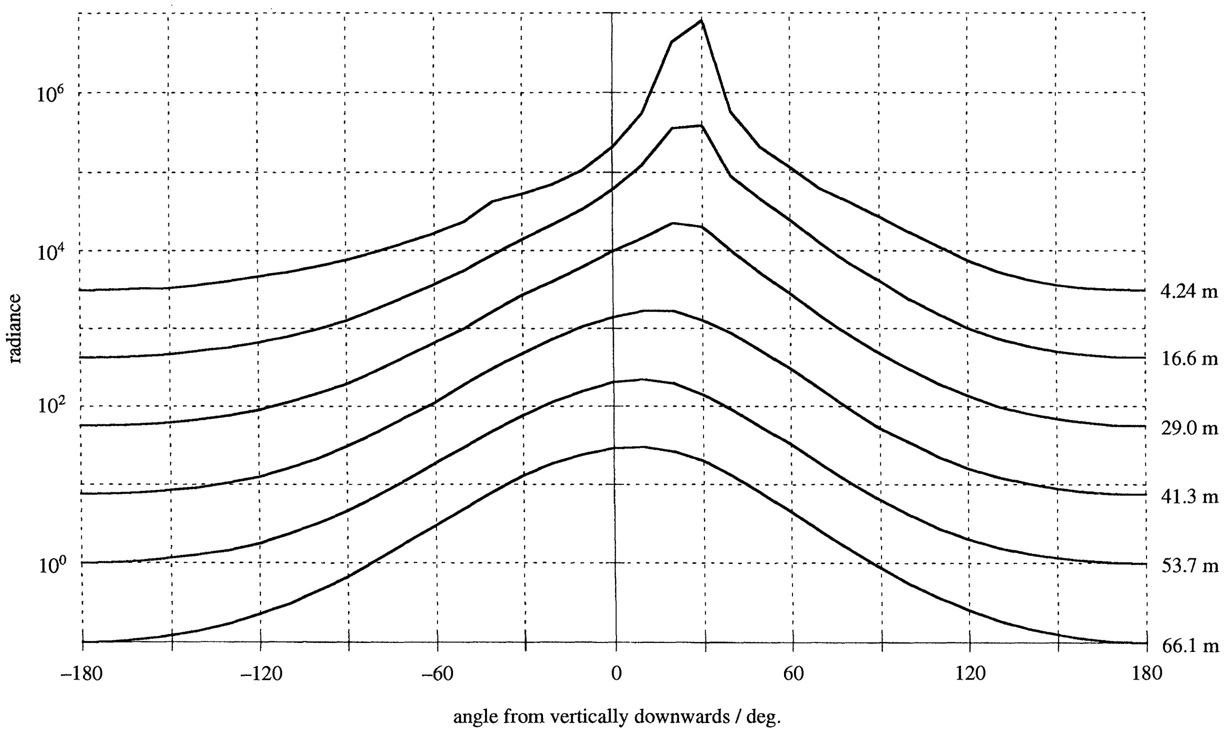

Figure 1. Radiance distributions, on a logarithmic scale, at various depths in a vertical plane containing the sun. After Tyler (1960) for Lake Pend Oreille, with the sun's altitude at 56.6°. These approximate more and more closely with increasing depth to a symmetric distribution around a vertical to the surface of the lake.

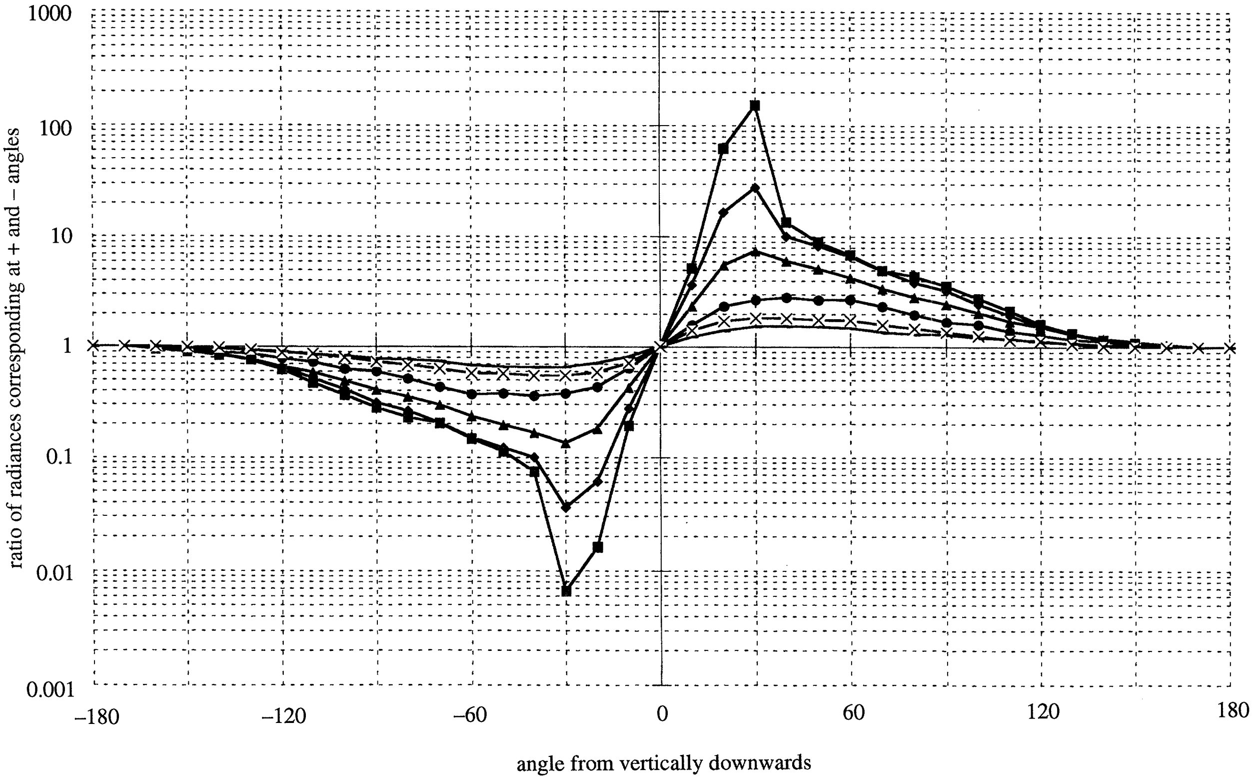

Figure 2. From the radiance data of figure 1. This shows, for various angles from the downward vertical to the surface of the sea, the ratios of radiances on the left- and right-hand sides of the plane perpendicular to that containing the sun. The different curves correspond to different depths: squares, 4.24 m; diamonds, 16.6 m; triangles, 29.0 m; circles, 41.3 m; crosses, 53.7 m; dashes 66.1 m. These ratios are those that would be found between the light falling on the left and right sides of a fish which maintained its back directed vertically upwards.

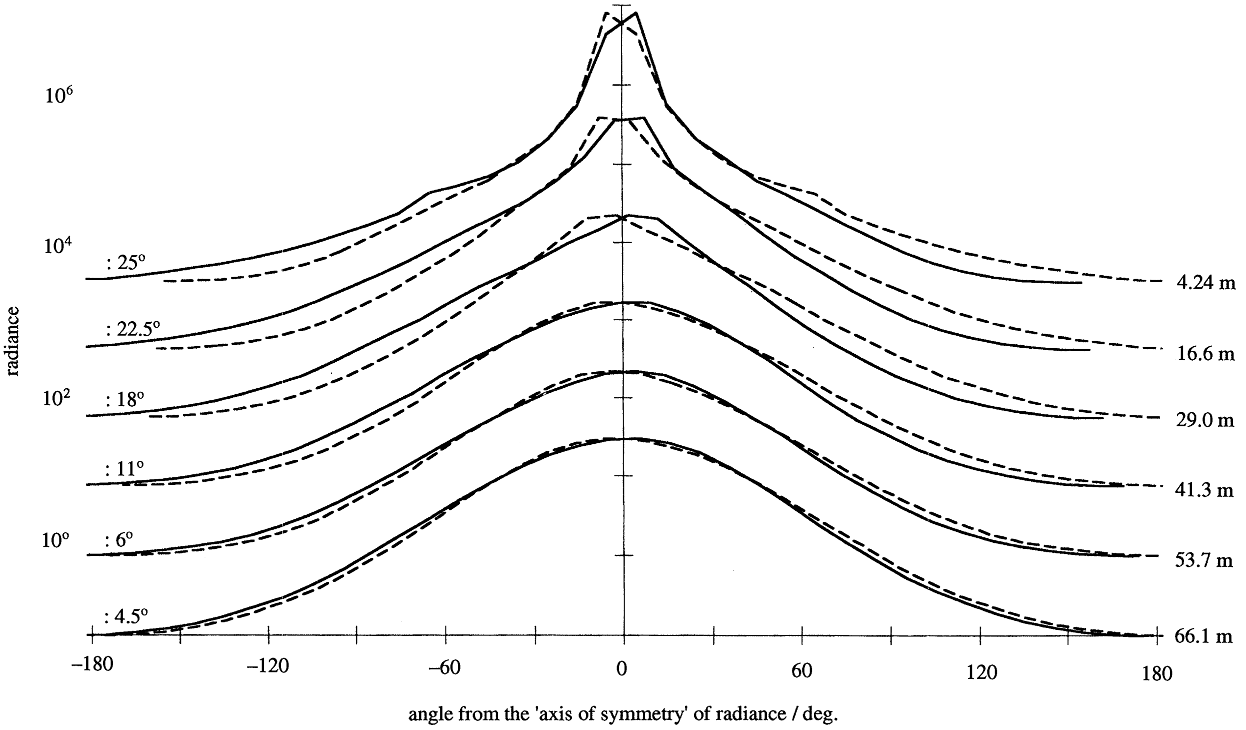

Figure 3. The radiance data of figure 1 on a logarithmic scale, but with each curve centred on an axis of symmetry and with each curve reflected left-to-right superimposed. Above the left-hand side of each curve, we give the values of the angle β (see figure 4).

fish is swimming quietly, the light distribution falls symmetrically on its left and right sides.

Figure 4*a* shows diagrammatically an asymptotic distribution of light. Figure 4*b* represents an angular distribution of light near to the surface of the sea in the plane containing the sun. OZ is an angle about which this distribution is almost symmetrical. The values of β (the angle between OZ and the downwards vertical) used for the curves in figure 3 are given above the left-hand side of each curve. It may be seen that these values are less than those to which a fish would need to tilt its body in order to direct its mid-dorsal line towards the brightest light. In terms of camouflage, this would be sensible. In general, the shadow which the fish would inevitably cast beneath itself would be diminished by extra reflected light. There are, moreover, relatively few positions that are in a cone around OZ containing only small values of ϕ from which the fish may be viewed and appear much darker than the background light.

Between different water masses, and between different wavelengths in a given water mass, the relative radiances in different directions depend on the balance between the absorption and scattering of light. In waters where scattering predominates, radiance will change relatively slowly with the angle ϕ; the upwardly directed light being a larger fraction of the downwardly directed light. In waters for which absorption predominates over scattering, the radiance distribution changes rapidly with ϕ, and polar diagrams like those of figure 4 are narrower 'ellipses'. However, comparison of measured and calculated distributions of radiances for a variety of natural waters, including oceanic, coastal and clear fresh waters shows that, for the waveband of light best transmitted, e.g. blue for oceans and green/yellow for coastal waters, the asymptotic angular distribution of radiance commonly have similar characteristics, showing a very rapid change of radiance with ϕ in the range 20° to 120°, with an approximate halving of radiance for every 10° to 20° increase in ϕ (Poole & Atkins 1937; Jenkin 1938; Jerlov & Fukuda 1960; Tyler 1960; Tyler & Smith 1970; Lundgren 1976 (cited by Jerlov 1976)).

Fish like the herring and mackerel will find as they pass from oceanic to coastal waters that although the waters become much less transparent the angular distribution of light changes relatively little: hardly at all in the green-yellow part of the spectrum.

Close to the bottom of the sea the picture is complicated by reflections, but such reflections will generally only have a significant influence over only a small fraction of the water column. Thus for waters for which the light falls to one-tenth for every 10 m increase in depth, the reflected light at 15 m from the bottom will be less than one-thousandth of the downward light. At only 5 m from the bottom, the reflected light will be less than one tenth of the downwardly directed light. It will, of course have a much more significant effect on the lower radiances of the upwardly directed light. The effects of light reflections from the sea bottom will be most significant where the sea is shallow and the water very clear, e.g. around coral reefs (see Partridge 1990).

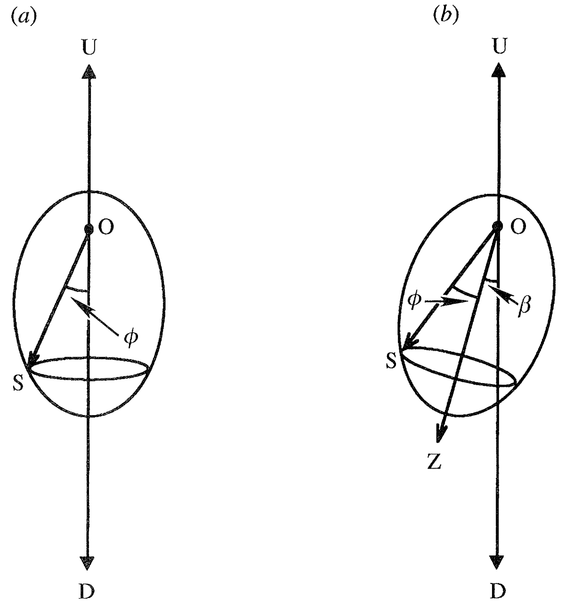

Figure 4. Diagrams illustrating the kinds of angular distribution of radiance which are assumed in the text. In the sea, the light is more directional than shown and the ratio of the radiances for directly upwards and directly downwards light is about 1:200 (see figure 1). (*a*) At a depth for which the final asymptotic distribution has been attained. For a given point, e.g. O, the distribution in three dimensions is given by rotating the curve S around the axis UD. The relative radiance in a given direction is given by the length of the line in that direction joining O to a point in the surface S. Angle ϕ is between a given direction and a vertical to the surface of the sea. (*b*) Diagram to show the meaning of angles ϕ and β for a radiance near the surface in a plane containing the sun, the approximate axis of symmetry of the light field (OZ) is inclined to the vertical (UD).

(*b*) ***The reflecting units***

Many fish are highly silvered and the platelets (the reflecting units) are quarter wavelength stacks of crystals and cytoplasm. They are typically around 100 μm^2 in area and about 1 μm thick. They differ from one another in different parts of the surface of the fish in their size, number per unit area, their orientations with respect to the body surfaces and in their reflectivities, including spectral reflectivities (see Denton & Nicol 1965*a*,*b*, 1966; Denton & Land 1970). In some platelets the optical thicknesses of the crystals and the spaces between them are almost constant and these platelets are highly coloured. Typically, such a platelet's spectral reflectivity, and the degree to which it polarizes light, will change with the angle of view. The maximum reflectivity moves towards shorter wavelengths as the platelet is viewed more obliquely. Other platelets, for which the number of crystals is higher but whose thicknesses and spacing are less regular, reflect well throughout the visible spectrum at all angles of incidence (Huxley 1968; Land 1972). Some reflectors lie on or under the scales others in the skin. They sometimes overlie white scattering layers; sometimes they are associated with pigmented layers.

(*c*) *The effects of fish movements*

We describe the movements of fish in terms of combinations of three components: (i) rolling, either to the left or right; (ii) pitching, the fish either diving or ascending; and (iii) yawing, a change in the heading of a fish, or part of a fish, with respect to the observer.

On figure 5 we show, as a basis for discussion, a pattern of reflecting platelets in the surfaces of a 'fish'. The shapes of actual fish and the orientations of their platelets are more complicated but this model fish has some features that are commonly found (Denton & Nicol 1966). On the central flank, F, the reflecting platelets have their flat surfaces parallel to the surface of the fish. Assuming an asymptotic light distribution, then these platelets are also perpendicular to the surface of the sea. On the inclined lower flanks, VI, the platelets are tipped away from the surface of the fish so as to be perpendicular to the surface of the sea and at the same time turned towards the tail. These platelets overlie a white diffusing layer. On the inclined dorsal surface, DI, the platelets are similarly arranged but these platelets overlie a dark pigmented layer.

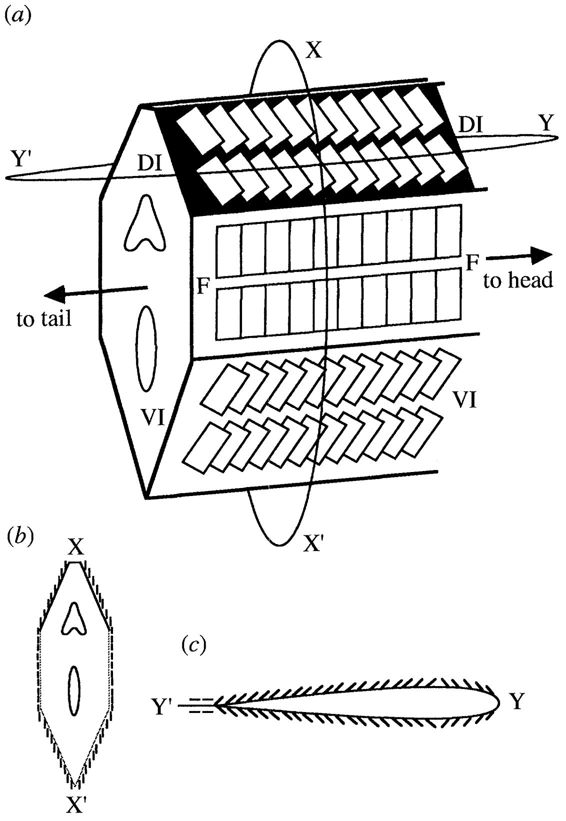

Figure 5. (*a*) Diagram of the orientation of reflecting platelets on the surface of a 'model' fish. On the flank (F) the platelets have their flat surfaces parallel to the surface on which they lie. On the dorsal inclined surface (DI), the platelets have their surfaces perpendicular to the surface of the sea, but are also inclined towards the tail. These platelets overlie dark pigmented layers. The ventral inclined surface (VI) is similar to (DI) but here the platelets overlie a white diffusing layer. (*b*) Section through the fish shown in (*a*) in the plane marked XX′. (*c*) Section through the fish shown in (*a*) in the plane marked YY′.

Let us take the angular distribution of radiance, calculated by Tyler for which the radiance falls approximately exponentially over a wide range of angles. Imagine that a fish acting as a perfect two-sided plane mirror is placed with its reflecting surfaces vertical in such a light field. It will then be invisible from all points of view. If it now rolls to an angle ξ to the vertical (see figure 6), one side of the fish will now appear brighter than all of the backgrounds against which it can be viewed, whereas the other side will appear darker than all possible backgrounds. This will be a very big effect for, over a wide range of angles of viewing, a roll of the fish of around 6° will make one side of the fish about twice as bright as its background whereas the other side becomes about half as bright as its background. For a given angle of roll the ratio of the change of brightness to background brightness will, for small rolls, change relatively little with angle of view over a large fraction of the possible points of view. (For a treatment of the relevant geometry, see Denton and Nicol (1965*b*), particularly their text-figure 9). It is probably safe to assume (see the later discussion on incremental thresholds) that, for a fish like the herring, a roll of the body of only a few degrees sustained for say 30 ms would be easily detected by a neighbouring fish in a school. For such a neighbour to the side of a rolling fish the whole width of such a fish would become brighter or darker than the background depending on the direction of the roll. As a sensory signal this has the great merit that the incremental increase or decrease in brightness divided by the background brightness will not change greatly over a wide range of viewing positions.

Let us now consider the effects on our model fish of pitching, i.e. either diving or ascending, without at the same time rolling. If the fish dives, the surfaces of the reflecting platelets on the regions designated F in figure 5 will remain perpendicular to the surface of the sea and their brightnesses will remain constant and continue to match the backgrounds. However, the surfaces of the platelets in the regions VI and DI will be turned towards the surface. A dive or an ascent for which the long axis of the fish makes an angle ρ with what we might call the rest position (figure 7), will turn the platelets upwards by an angle τ defined by the equation $\sin \tau = \sin \rho \cdot \sin \epsilon_p$, where ϵ_p is the angle by which the platelets are tipped towards the tail (see figure 8, which also describes other angles defining the orientation of platelets). If ϵ_p is only 20°, the effect will be a third of that found for a roll of 20°. If ϵ_p is 30° it will be about a half of that for a 30° roll and with the angular distribution of the type shown in figure 1, a dive of only 12° can double the brightnesses of parts VI and DI of the fish with respect to the background. If the fish ascended, parts VI and DI would darken with respect to the background and the effect would still be dramatic.

Finally we consider the effects of yawing movements: let us suppose (figure 9) that a surface, similar

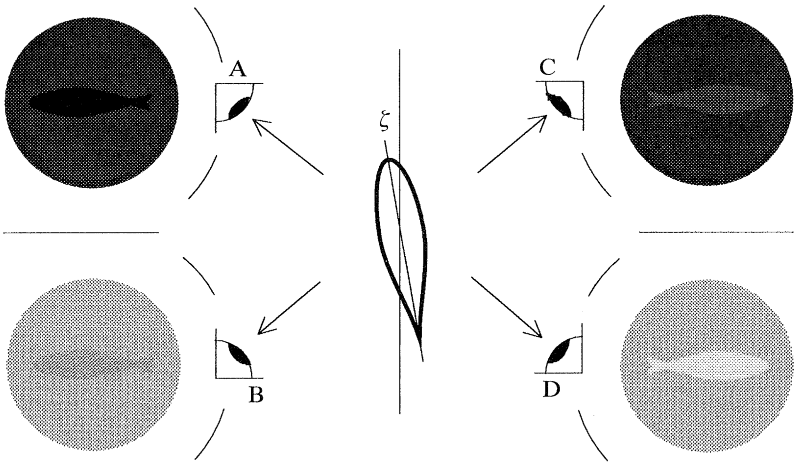

Figure 6. Diagram showing the kind of image that a silvery fish, treated as a perfect plane mirror, presents to an external observer when its body is rolled away by an angle ξ from the vertical where it would have matched the background. An observer A above will see the fish against a dark background, whereas an observer B below will see the fish against a light background. For both observers, the fish will appear darker than its background and the ratio of difference in brightness between fish and background (ΔI), divided by the background brightness I will be about the same and so, provided that the light levels are not too low, the fish will be equally visible to both observers. Observer C is similar to Observer A, and Observer D is similar to Observer B, except that for Observers C and D, the fish will appear brighter than its background.

to surfaces DI or VI on the 'fish' of figure 5, is viewed by an observer. When the angle γ (figure 9*a*) is less than twice the angle ϵ, the surface will be darker than the background, for the reflected light will then come not from the platelets, but either from the dark layer beneath the platelets of surface DI or from the white layer beneath the platelets of surface VI; this surface reflects from smaller values of ϕ and so is also dark. When γ is greater than 2ϵ the surface will appear as bright as the background. The region F on our hypothetical fish will have a brightness that is independent of γ.

Figures 10 and 11 show diagrammatically the kind of effects on the overall appearance of an observed fish caused by changing the angular relations between the observed fish and eye of an observing fish.

In the next section of this paper we describe experiments and observations made on the greater sand eel, a fish which commonly moves sharply upwards and downwards as well as in the horizontal plane, and on the pollack (*Gadus pollachius* L.). In both species the numbers and properties of the crystals forming the platelets are such that the platelets reflect a broad band of wavelengths and the reflectivities of the various surfaces remains high at all angles of incidence. They do not have the complication found in some other species, for example in the herring (*Clupea harengus* L.) or the horse mackerel (*Trachurus trachurus*) (on which we shall report later) for which there are, in some parts of the fish, highly coloured reflecting layers.

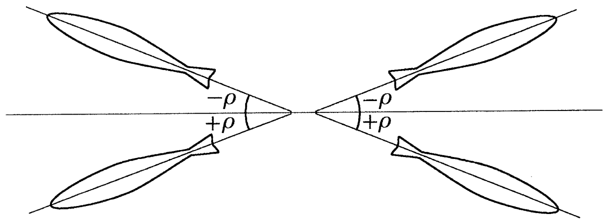

Figure 7. Diagram illustrating the meaning of the angle ρ. This is positive for all dives and negative for all ascents.

2. MATERIALS AND METHODS

(*a*) *Materials*

The experimental work was done on fish freshly killed by being placed in a suitable solution of the anaesthetic 2-methylbutan-2-ol (tertiary-amyl alcohol) until respiratory movement of the operculum and reflex response to touching the tail had ceased for several minutes.

(*b*) *Methods*

Measurements of the orientations of silvery layers were made with the apparatus, shown in figure 12 (similar to that described by Denton *et al.* (1972) on their figure 4). A whole fish, or part of a fish, was held lightly by elastic bands on a transparent Perspex platform in a rectangular chamber; the platform could be positioned in any desired plane by rotations around two axes. The chamber was filled with seawater. An approximately parallel beam of light

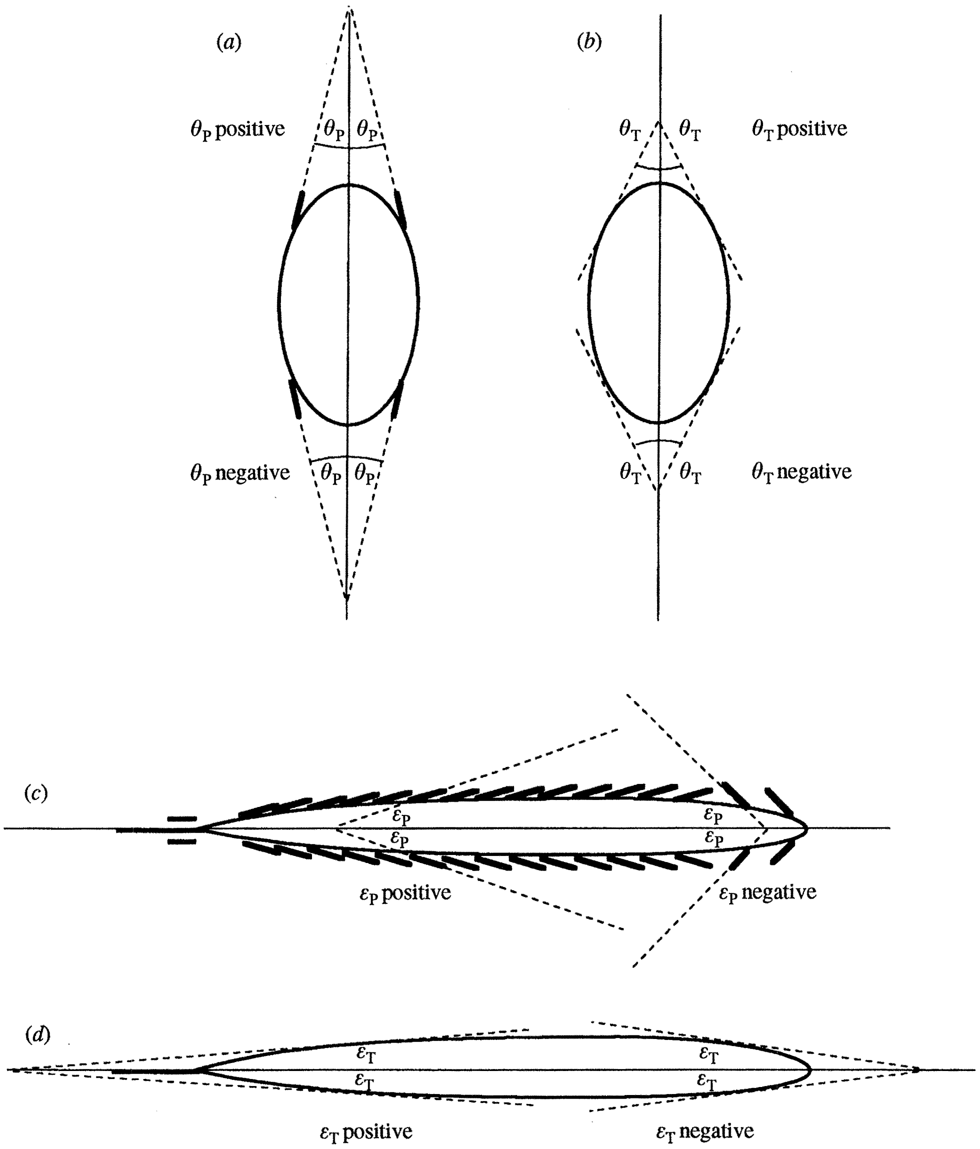

Figure 8. Diagram to show the meaning of the symbols θ_P, θ_T, ϵ_P, ϵ_T used to describe the orientation of a reflecting platelet. (*a,b*) 'Vertical' sections through a fish perpendicular to its anterior-posterior axis. (*c,d*) 'Horizontal' sections through a fish perpendicular to the plane containing its mid-dorsal and mid-ventral lines. θ_P and ϵ_P are the angles between the surface of the platelet and the mid line of the fish, θ_T and ϵ_T are angles between the tangents to the surface of a fish and the midline. The angles θ and ϵ defining the orientation of a platelet with respect to the surface on which it lies are given by the equations $\theta = \theta_P - \theta_T$ and $\epsilon = \epsilon_P - \epsilon_T$.

was made to fall on the fish along a line perpendicular to one side of the chamber and the fish was observed along a line very close to that whence the light came. To find the orientations of the silvery layers on a particular area of the fish's surface the angular settings giving the brightest reflections for this area and the corresponding area on the other side of the fish were found. These settings, together with those for the brightest reflections found for pieces of aluminium foil wrapped around the fish close to the area under study and for flat mirrors placed on the platform, gave all the information needed to estimate the angular settings of both the surface of the fish and the reflecting platelets (see Denton & Nicol 1965*a,b*).

On figure 13 we show diagrammatically an apparatus used to simulate approximately an angular distribution of light of the kind found in the sea. This was used for observations of the changes in the patterns of brightness of the external surfaces of fish produced by changes in their orientations. A Perspex chamber of dimensions 27 cm × 27 cm × 30 cm high was filled with seawater. The fish to be studied was attached to a transparent platform whose orientation could be set at known angles of roll, pitch and yaw. Four panels of opalized plastic sheet were placed inside the chamber against its side walls and these were illuminated by four small fluorescent tubes partly covered by opaque strips of wood. Observations and photographs of the fish under study could be made through a slit-shaped opening in one of the panels. By adjusting the positions of the fluorescent tubes and the strips of wood covering them, the illumination of the four panels could be made almost identical. Measurements of the brightnesses of small areas of the opal panels with a S.E.I. photometer showed that the brightness of these panels fell by a

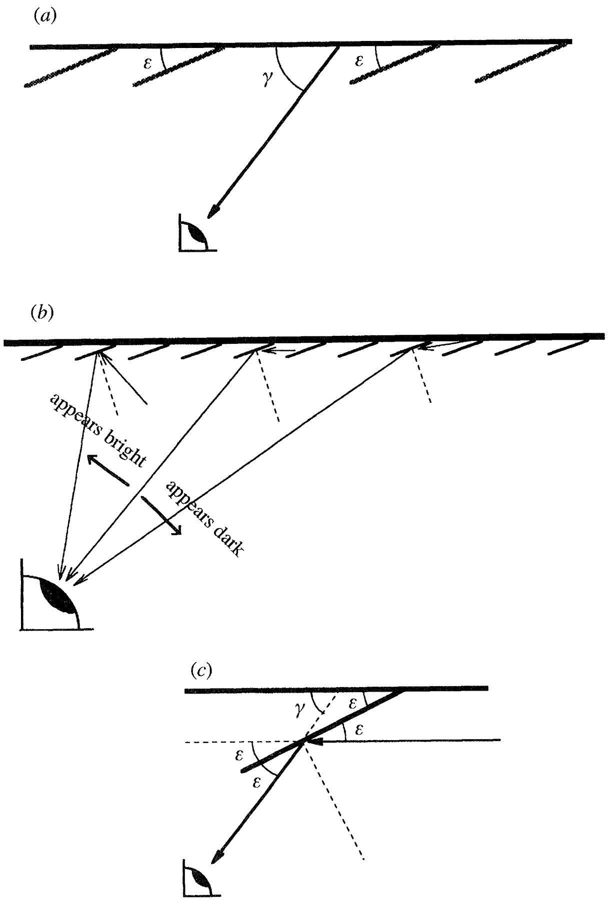

Figure 9. Diagram showing yawing effects. (*a*) The surface is viewed from an angle of γ, and has its reflecting platelets set at an angle ϵ to the surface. (*b,c*) If the angle γ is less than 2ϵ, the reflection will come from the underlying pigmented surface and will appear dark; if the angle is greater than 2ϵ the observer will see light reflected by the platelets.

factor of ten from the bottom to the top of the panels. The rate of fall of brightness from bottom to top was progressive but not uniform, the brightness falling more quickly over the lower (brighter) parts of the panels. This corresponds roughly to what happens in the sea. Confirmatory measurements were made on the brightness of mirrors placed close to the position at which the fish were photographed. Thus, apart from being upside down (a complication easily overcome by placing the fish upside down), the field of light around an object placed in the centre of the chamber approximated roughly to that found in the sea.

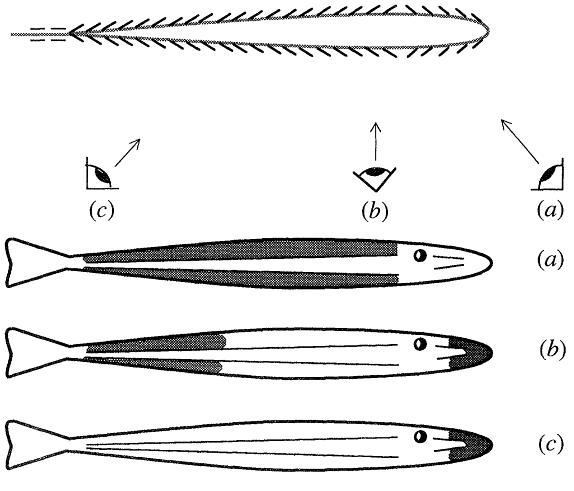

Figure 10. Diagram showing how the appearance of a fish with reflecting layers oriented like those of the 'model' fish of figure 5 varies with the relative position of the fish and the observer. Hatched areas are dark.

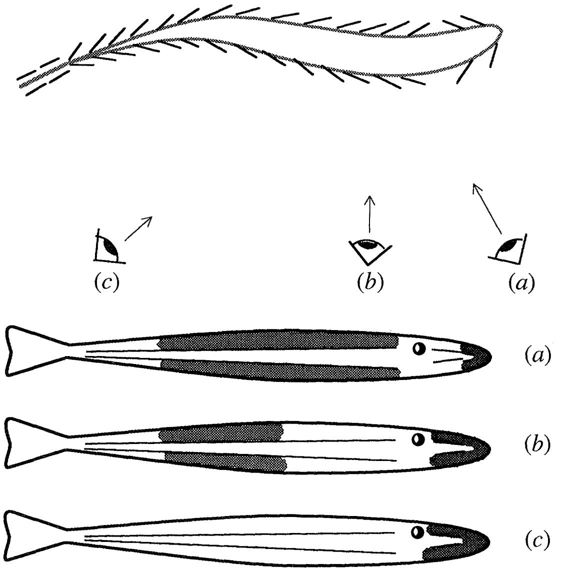

Figure 11. Similar to figure 10, but with the observed fish making swimming movements.

3. RESULTS

In figure 14*a*, we show the position of a section across a sand eel, shown in more detail in figure 14*b,c*. In life the silvery layers are conspicuous, particularly on the lower flanks. The dorsal region, D, which we have not studied in detail, shows interleaved narrow silvery and dark bands which run diagonally around the dorsal part of the fish (see figure 17). The silvery bands become more conspicuous when the fish is viewed from its tail, whereas the dark bands dominate when the fish is viewed from its head. Immediately above the lateral line is a band, T, characterized by being

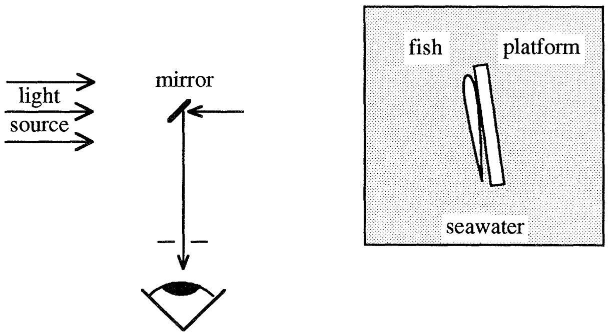

Figure 12. Diagrams of the apparatus used to measure the angular dispositions of the reflecting platelets in the surfaces of fish. The fish is held against a transparent platform that can be set at any desired orientation within a chamber filled with seawater. The chamber is illuminated from a distant light source (a car head light), and with the aid of a mirror the fish is viewed from approximately the direction from which the light strikes the fish.

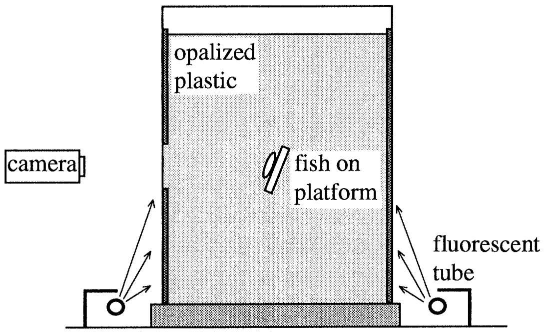

Figure 13. Diagram of the apparatus used to simulate a distribution of light which, apart from being upside-down, roughly corresponds to that found in the sea for a fish placed near the centre of a chamber. The chamber is filled with seawater and the fish can be set at any desired orientation. Sheets of diffusing opalized plastic are placed inside the walls of the chamber; an opening has been made in one of these sheets through which the fish can be viewed or photographed. The walls of the chamber are illuminated by small fluorescent tubes.

'scalloped'. This area is silvery but a little orange-yellow in colour. Below T there is a broad very silvery band which we have arbitrarily divided into an upper part, C1, and a lower part, C2. The lowest band on the flank, B, is divided along its length into sections of the same width as the scallops of band T. Within all of these bands it is easy to see lines indicating the directions of the long axes of the reflecting platelets. When viewed from below the major part of the ventral surface is matt white but there are two narrow specularly reflecting bands V, one on either side of the midline of the fish.

It proved easy to obtain a good idea of the orientations of the reflecting platelets by some simple experiments. A fish was held lengthways on a platform which could be rotated around its long axis. A strip of bright aluminium foil was wrapped around the fish close to the position for which we wished to determine the approximate orientations of the reflecting platelets in the various bands listed above. The fish was illuminated with a directional light source and both the positions of this source and the direction from which the fish was viewed or photographed could be varied (figures 15 and 16). For bands T and C the settings for which the foil and fish gave the brightest reflections were close to each other. As the fish was turned around its long axis a narrow bright band which approximately coincided for the fish and foil moved around the fish from band T to the most ventral part of band C2 (see figure 15). This showed that for these bands the flat surfaces of the platelets were close to being parallel to the surface of the particular part of the fish on which they lay. This was not the case for bands B. Bright reflections could only be obtained from these bands by having the direction along which light was incident and the direction of viewing both coming from the tail end of the fish (see figure 16). This shows that the surfaces of the platelets of band B are inclined towards the tail of the fish. The angular positioning of the platform which gave the brightest reflection indicated that the surfaces of the platelets of band B were turned so that they would be almost perpendicular to the surface of the sea if the fish were swimming with its back and long axis parallel to the surface.

More accurate measurements of the orientations of

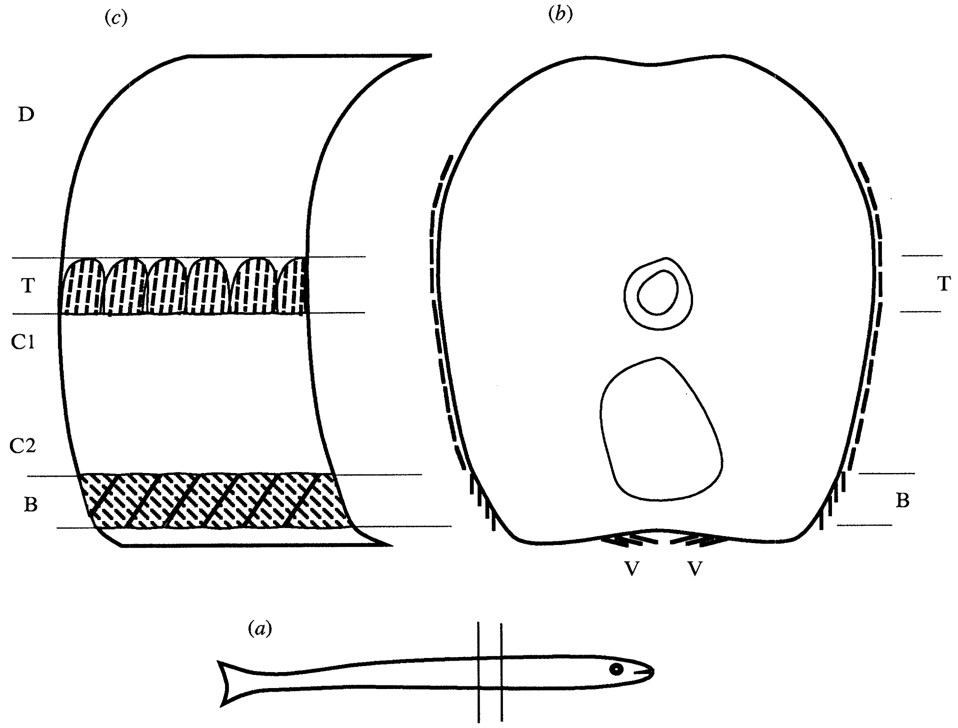

Figure 14. *Hyperoplus lanceolatus*. (*a*) Positions where two transverse cuts were made across the fish; (*b*) shows a view of the cross-section of the fish, and (*c*) a lateral view. The letters D, T, C1, C2, B and V define the longitudinal bands described in the text. The short black lines show the orientations of the reflecting platelets.

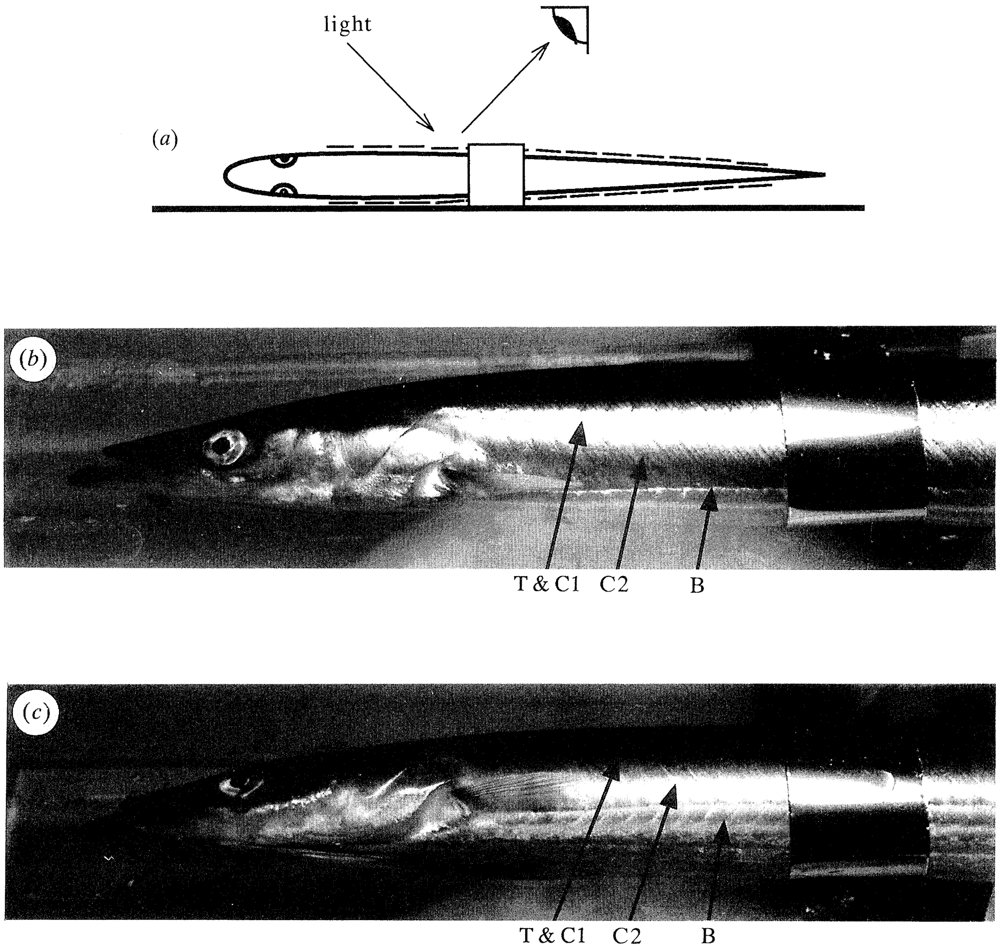

Figure 15. (*a*) Diagram of fish lying on a platform which can be rotated around its long axis. The light is incident from the rostral end of the fish, while the fish is viewed from its caudal end. A piece of bright aluminium foil has been wrapped around the fish. (*b*) Photograph of a fish; the platform has been rotated to the setting for which the bands T and C1 gave their brightest reflections. This coincides with the setting for which the adjacent foil does so too. (*c*) Similar to (*b*), but the fish has been rotated so that band C2 gave its best reflection: this again coincided with the best setting for the adjacent foil. Note that the band B stayed dark.

the reflecting platelets in the various bands T to V on the surface of the sand eel were made with the apparatus shown on figure 12. We shall define the orientation of a body, or platelet surface, by the angles θ and ϵ (see figure 8). In table 1 we give measurements of the values of angles θ and ϵ for the surface of fish and for pieces of aluminium foil wrapped around the fish. The values given for fish B are the means of measurements made by two observers. The differences between their measurements were small: on the average less than 1° with most pairs of measurements agreeing to better than 3°. In figure 14, we show diagrammatically the orientations of the surfaces of the reflecting surfaces and the surfaces on which they lie on cross sections through the fish. In making this diagram we have drawn on further measurements and observations showing that the same pattern of reflectivity obtains for most of the length of the fish from the operculum to close to the tail. Near to the tail the silvery region of the flank corresponding to the bands T to B has fairly uniform reflecting properties with angles θ of approximately 7° and angles ϵ of around 10°. Like other fish the reflecting surfaces are not completely specular, the range of angles from giving practically zero reflection to giving the maximum reflection being about ±10°.

The boundary between bands C2 and B in terms of the angle ϵ is not always sharp. Sometimes the lower parts of band C2 have larger average values for ϵ than is usually the case. This accounts for the difference between the 17° and the 4° found for ϵ for fishes A and B of table 1.

With the above measurement in mind, we shall now describe the results obtained with the apparatus of figure 13 in which the fish is viewed in a light environment approximating that of the sea.

Figure 17 shows the effects of roll. For zero roll (0°) band T and band B are approximately equal in brightness whereas the brightness of C falls as we move from the midline downwards. This is what we might expect from the orientations of the platelets. Those in band T will, at the 0° setting, have their reflecting surfaces perpendicular to the surface of the sea and so do those of band B. The platelets in band C which follow the curve of the body of the fish, become progressively turned downward as we move around the body from T to B, and so reflect light from less and less bright parts of the surrounding light field. As the

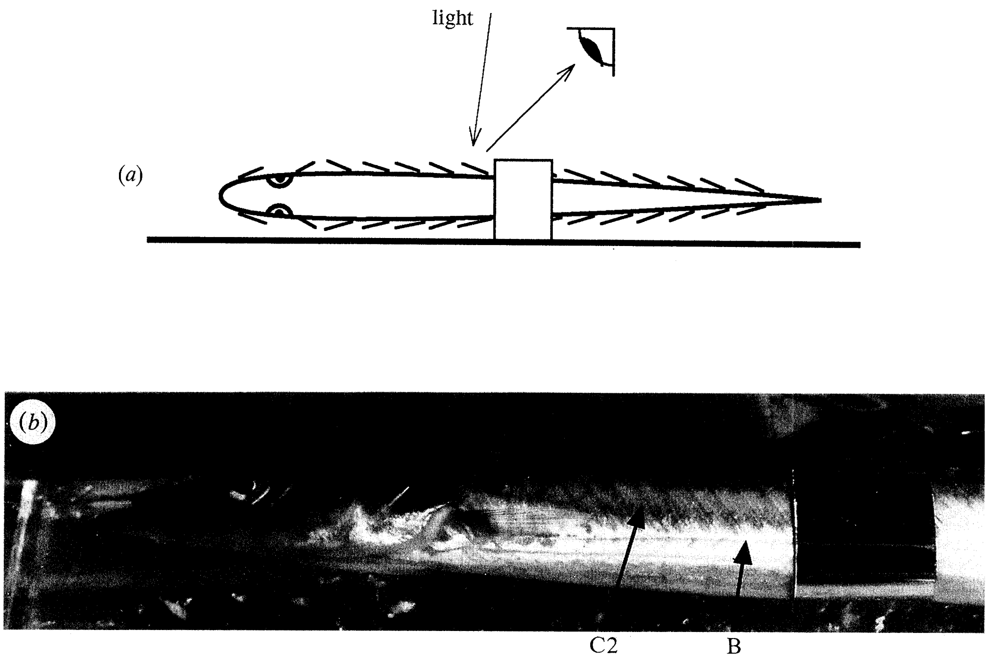

Figure 16. Similar to figure 15. To have a bright reflection from the band B of the fish, the directions of the incident light and the point of view have both to be from the caudal end of the fish. This is because the reflecting platelets are tipped towards the tail in band B. The foil now appears dark. Note that at the head end of the fish, the platelets are tipped towards the snout.

fish rolls all parts of the reflecting system becoming brighter together as the side is turned towards the surface, i.e. going from 0° to +10°, and all parts become dimmer together as the side turns downward, i.e. going from 0° to −10°.

Figure 18 shows the effects of pitching. The C bands are little changed by going from ascending at an angle of 45° to diving at 45° whereas the B band becomes darker on ascending and much brighter on diving (compare with the photograph for 0° of figure 17). This is in accord with the fact that the platelets of band B are turned towards the tail. Figure 19 shows the effects of rolling and pitching at the same time.

We shall now examine the consequences of yawing movements. These are most easily seen in figures 18 where both the band B and the dorsal area above band T are brighter at their anterior ends. This is what we should expect because in both the reflecting platelets are tipped towards the tail. On figure 20 we show the dramatic difference in the reflectivity of the dorsal part of the body of a young pollock of pitching from 45° to −45°.

Table 1. *Orientations of some body surfaces and reflecting platelets of the greater sand eel*

position on fish (see figure 14)	foil[a]		fish[b]		fish-foil[c]	
	θ_T/deg.	ϵ_T/deg.	θ_P/deg.	ϵ_P/deg.	θ/deg.	ϵ/deg.
fish A						
T	−2	2	−1	6	1	4
C1	4	2	3	8	−1	6
C2	26	3	25	17	−1	14
B	32	5	5	25	−27	20
fish B						
T	−8	3	−7	2	1	−1
C1	5	2	3	3	−2	1
C2	27	2	25	4	−2	2
B	36	0	0	21	−36	−21
V	72	−5	61	10	−11	15

[a] Foil: measurement on foil, giving angles θ_T and ϵ_T defining the external surfaces with respect to mid-planes of the fish (figure 8*b*,*d*).

[b] Fish: measurement on reflecting surfaces (platelets) of the fish giving the angles θ_P and ϵ_P defining the surface of the platelets with respect to the mid planes of the fish (figure 8*a*,*c*).

[c] Fish-foil: differences θ and ϵ between corresponding values of footnotes (b) and (a) giving the orientation of the platelets with respect to the surfaces on which they lie.

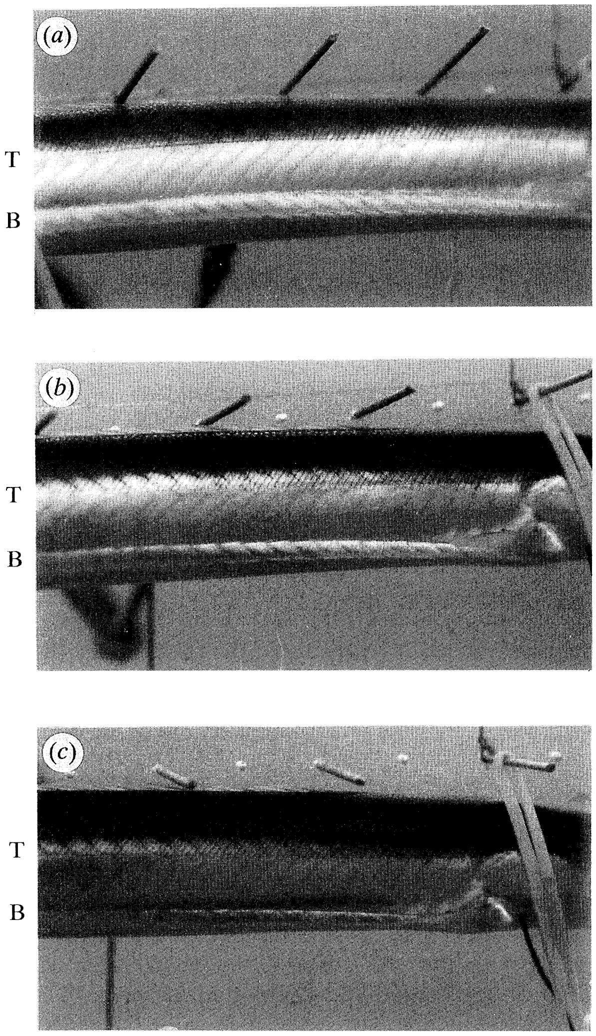

Figure 17. *Hyperoplus lanceolatus*. Photographs taken in the apparatus shown in figure 13 showing the effects of rolling. The angles of roll are: (*a*) +10°; (*b*) 0°; and (*c*) −10°. The anterior end of the fish is to the right-hand side. It can be seen that the various bands all become brighter and darker together. This is a large effect. The brightness of the surface of the fish approximately doubles or halves for every 10° of roll.

The qualitative tests described above show that the changes in brightness that were predicted from the disposition of the reflecting platelets will be found in the sea.

After death, the tissues around the reflecting platelets become progressively less and less transparent, and the platelets themselves become less regularly oriented. However, the experiments described here were made soon after death and our observations showed that apart from fairly rapid changes which sometimes occur in the darkness of the dorsal regions, the appearance of the fish hardly changed during the time needed to complete the experiments.

4. DISCUSSION

The hypothesis that we are testing is that silvery fish can send messages in a code whose symbols are transient patterns of bright and dark patches on its body.

There is no doubt that, when silvery fish like the herring are swimming very slowly, the reflections from their external surfaces make it possible for the fish to match the backgrounds of natural light in the sea. This invisibility depends on the penetrating daylight falling symmetrically around the fish's body and such a fish swimming in mid-water can only conceal itself in this way by not rolling or pitching more than a few degrees. The kind of fish that are probably the best of all in achieving invisibility are the deep sea hatchet fish. They not only have dark dorsal surfaces and silvery sides and a sideways compressed body, but they also emit light from their ventral surfaces to avoid casting a shadow. They have been shown by Jannsen *et al.* (1986) to have a very special arrangement of their musculature to allow them to keep their ventral surfaces horizontal and so preserve their camouflage when swimming downwards in the sea. In a more general way, there may well be advantages from the point of view of concealment in species like the horse mackerel and John Dory moving by means of the fins rather than by movements of the body.

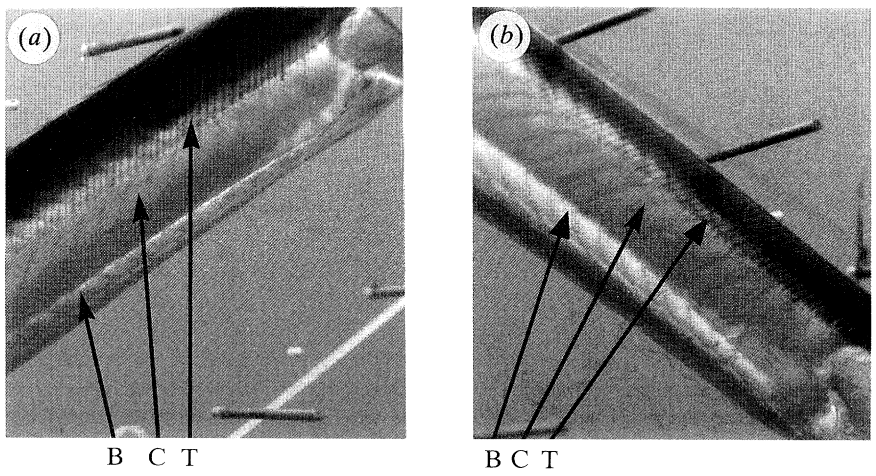

Figure 18. Similar to figure 17, but showing the effects of pitching with zero roll. (*a*) Ascending; (*b*) diving. It can be seen that the brightness of bands C and T changes relatively little, whereas the brightness of band B changes a great deal between the fish ascending and diving.

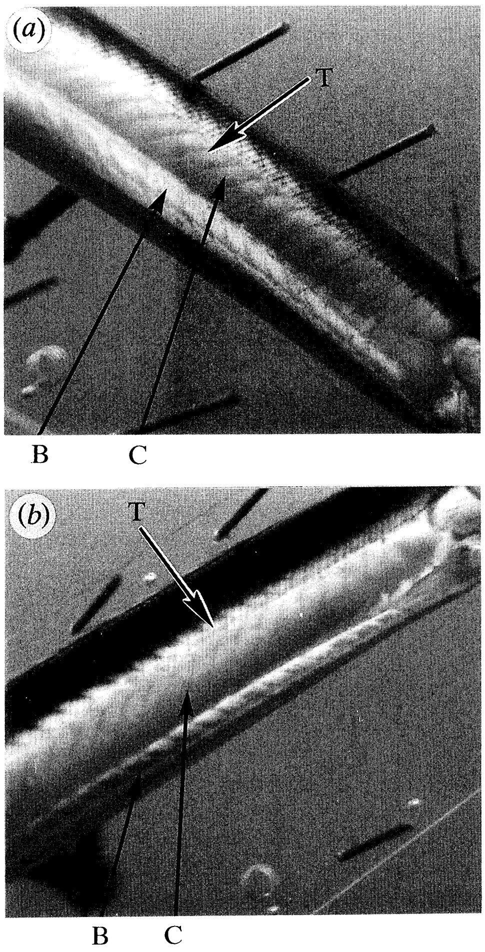

Figure 19. Similar to figure 18, but showing the effects of simultaneous pitching and rolling. (*a*) Diving, rolling +10°; (*b*) ascending, rolling +10°.

In the preceding sections, we have shown that, in some fish, very great changes in brightness over large fractions of their body surfaces are produced by quite small movements, for examples rolling or pitching by only 5° to 10°, and that different patterns of brightness of the fishes' external surfaces accompany different movements. Now it is universally recognized that vision plays a major role in the schooling of fish, allowing members of a school to make rapid, well-coordinated manoeuvres. It seems certain that the visual cues (signals) that make such manoeuvres possible must be provided largely by the changes in the patterns of brightness described above. Judging by our own observations, on fish swimming in tanks, and a study of video-recordings made in the sea, such changes are to us, and almost certainly to the fish, very much more visible than the changes in shape or position which they accompany, any detection of which must also depend on changes in brightness.

So far, we have only dealt with reflections from major areas of the surfaces of the fish. Fish often have however, quite small, specially reflecting areas for which signalling seems to be the only obvious function. Sometimes, these areas lie in tubes or depressions, e.g. in the lateral lines, so that the light that one of these specialized structures reflects can only be seen from particular directions contained in a small solid angle in the spare around the fish. Here we shall consider only the special case of signalling from the tail. Since the tail inevitably tilts away from the vertical in the course of swimming then, if being invisible were the overriding desirable adaptation, we might expect the region of the end of the tail to be unsilvered and perhaps transparent. In fact it is common for fish to have a 'silver' patch on both sides of the tail extending onto the rayed part of the tail. We have found such patches on the sand eel, the mackerel (*Scomber scombrus*), the horse mackerel (*Trachurus trachurus*), the herring, the pilchard (*Clupea pilchardus*) and the smelt (*Osmanthus eperlanus*). Dr C. S. Wardle tells us that the skipjack (*Euthynnus pelamis*) and the yellowfin tuna (*Thunnus albacares*) have brilliant blue patches above the caudal peduncle. A photograph of a patch on the tail of a pilchard is shown on figure 21. This photograph was taken with side lighting and does not represent the appearance of the fish under natural lighting conditions. The surfaces of the reflecting platelets of such patches are approximately vertically oriented when the tail is vertical. They will, therefore, in the natural lighting found in the sea match the background so long as the tail remains vertical. However, when the fish swims the tail must twist (roll) first one

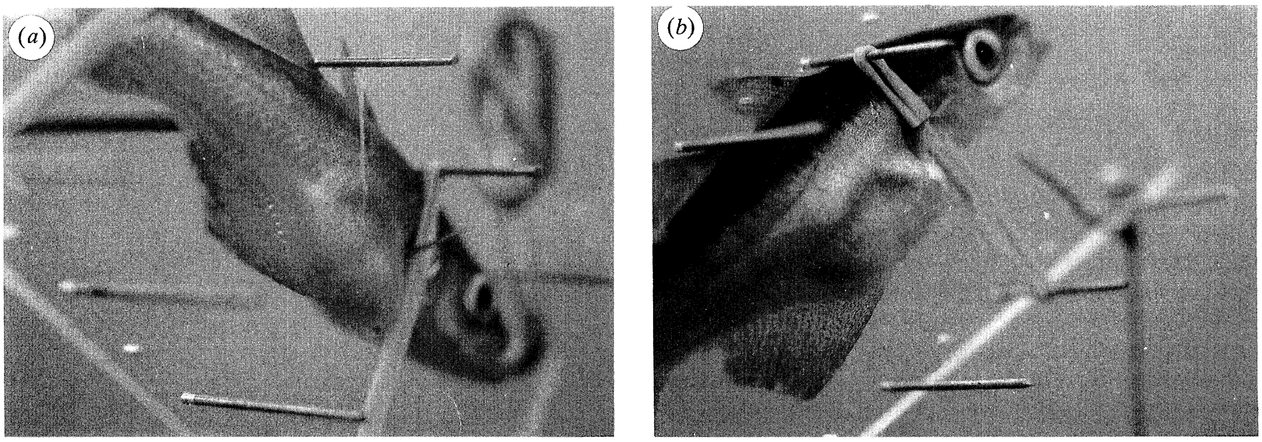

Figure 20. Similar to figure 18 but for a small pollock. (*Pollachius pollachius*). (*a*) Diving; (*b*) ascending. Here, the most striking effect is in the dorsal regions.

Figure 21. Photograph of the bright tail-spot of a pilchard (*Clupea pilchardus*); taken in the laboratory.

way and then the other way and an alternating series of bright flashes and what we may describe as 'dark flashes' will be emitted. It might be thought that flashes of the type just described would make the fish very conspicuous to predators but as we shall argue later this is unlikely to be the case and that small flashing areas although very conspicuous to near neighbours will not be seen by predators at, say, ten fish lengths. The tail of a fish like the herring does in fact sometimes roll through considerable angles. Figure 22 shows two high-speed video images of two herring swimming. One (*a*) is with the fishes swimming slowly, the other (*b*) is for one of the fish making a rapid turn. The conditions under which the records were made are given by Rowe *et al.* (1993). The images of the fish are silhouettes. The silvery patches which we have discussed above are to be found on the thin parts of the tail (easily identified in figure 22*a*). As photograph (*b*) shows, during the rapid turn this part of the tail turns through large angles and so it must emit dramatic bright and 'dark' flashes. We note that in the herring these areas of the tail are equally silvery as in the pilchard, but they are less distinctively separate patches. Some silvery fish have several small silvery structures which will be very conspicuous to neighbouring fish from only a limited range of positions. There are often brightly coloured patches on the head and on the operculum. Perhaps these signal information to neighbours when the fish are feeding.

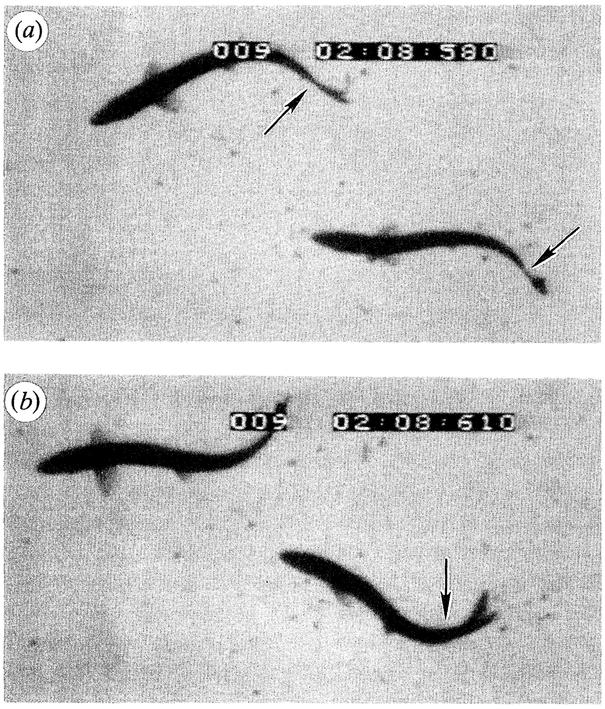

Figure 22. High-speed video-recordings of two herring made in the Dunstaffnage Marine Research Laboratory, made by Dr R. S. Batty. (*a*) the fish are swimming slowly, the caudal peduncles (arrowed) are vertical and appears as very thin silhouettes. (*b*) the lower fish is making a rapid turn and the tail has rolled through about 60° in 30 ms.

On figure 23, we show copies of frames from a video recording made in the sea just beyond the breakwater of Plymouth Sound. The recording was made by Dr G. W. Potts who very kindly gave his permission for these frames to be reproduced. They show reflections from the side of a greater sand eel as it swam across the field of view. Four of the frames (*a*–*d*), taken at 40 ms intervals, show the fish invisible in (*a*), appearing in (*b*) and (*c*), and disappearing again in (*d*). On viewing the original recording of the moving fish, it is easy to see that bright and dark flashes move along and across the faint outline of the image of the fish (see figure 21*e*) indicating that this fish rolls as it swims. This is not surprising for it has a fairly well rounded body (figure 14) offering less resistance to roll than the laterally flattened body of a fish like the herring.

So far we have made little mention of the two reflecting bands V shown on figure 14 for which the orientations are given in table 1. These will only give bright reflections when the fish is making steep dives. It seems impossible to conceive that these have any other role than that of communicating information to neighbours. They are even smaller bands than the B bands and so will have a very limited range for which they will be conspicuous.

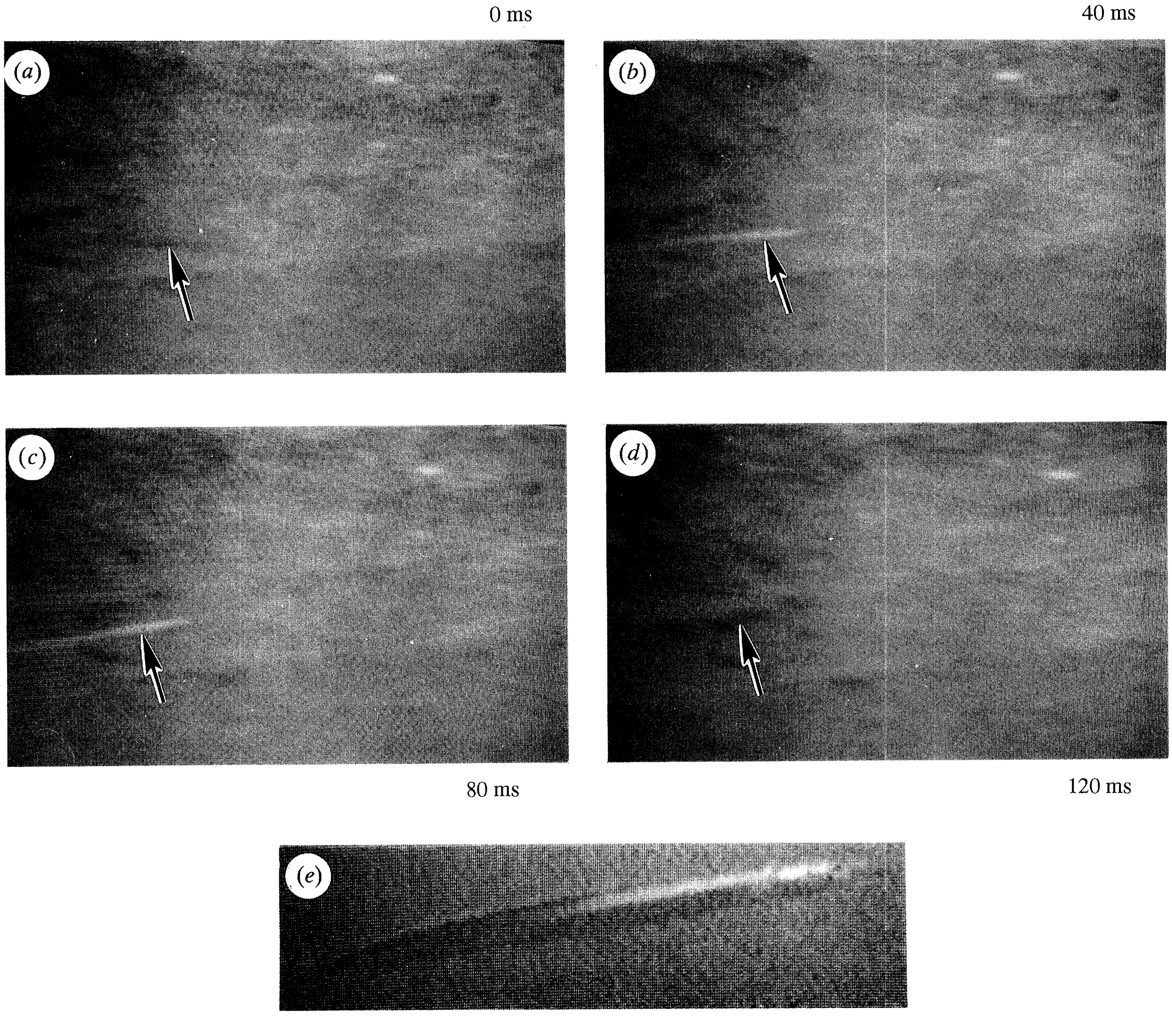

Figure 23. Video recordings made in the sea off Plymouth by Dr G. W. Potts showing a sand eel (*Hyperoplus lanceolatus*) swimming across the field of view. (*a–d*) Four successive frames, 40 ms apart; the fish is very difficult to see on (*a*) and (*d*), but very visible by the light which it reflects on (*b*) and (*c*); (*e*) is a closer view of the fish showing a pattern which depends mainly rolling and ascending.

(*a*) *The visibility of the signals*

In the absence of adequate data on the performance of the visual systems of fish it seems worthwhile considering the flashes that will be produced by silvery fish in relation to our own vision. We shall base our analysis on the excellent studies of incremental thresholds made by Barlow (1958). His papers give a clear account of the extensive literature on this subject. He measured the incremental intensities (ΔI) of patches of light of various areas and durations that would just be visible to the dark-adapted human eye against backgrounds covering a wide range of intensities (I). He used only green light of wavelength 507 nm. He measured intensities in quanta per square degree per second, entering an eye with an area of pupil of 3 mm^2. He worked with background values of log I5 up to 7.83. It is easy to show that this is close to the intensity of light found by Kampa (1970) for an observer looking sideways ($\phi = 90°$) at about 200 m depth in oceanic waters for the waveband of width about 50 nm around the blue light of wavelength 475 nm which penetrates these waters best. At the surface of the sea, light of this waveband alone would be about 1000 times more intense and the daylight would not have been filtered by the sea and light of wavelengths covering the whole visible spectrum would contribute to I (see Tyler & Smith 1970). Nevertheless, considering the differences between oceanic and coastal waters and between different days and times of day the values of ΔI for the background log I of 7.83 (the brightest studied by Barlow) seem adequate for the present discussion. The incremental thresholds found by Barlow were those for which the flash had only a 80% chance of being seen and they were made by observers who knew where the 'flash' would be given against an unchanging background. They seem certain to be appreciably lower than those that would be required by a fish searching for a significant change in the pattern of light produced by a neighbour. Let us suppose that increments five times those found by Barlow would be required. Consider an observer whose eye is positioned at one fish length in the same horizontal plane and perpendicular to the 'signalling' fish. We confine our discussion to the three sources of stimuli

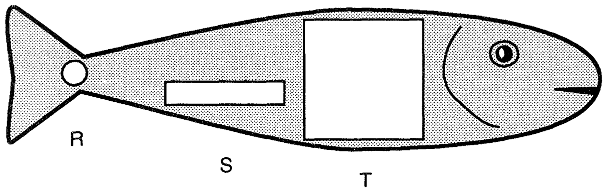

Figure 24. Diagram showing silvery regions used for signalling on a fish. Patch R is a silvery spot on the caudal peduncle, whose platelets are parallel to the surface of the fish and perpendicular to the surface of the sea like those on the region F of the fish shown in figure 5. On patch S, the platelets are oriented like those of region VI of figure 5, i.e. perpendicular to the surface of the sea, but tilted towards the tail. Patch T is like patch R, but much larger.

shown in figure 24, i.e. a patch T of area 25 square degrees on the body, a patch R on the caudal peduncle of 1 square degree (this is a little larger than the patches shown on figure 21*a*) and a strip S of area 5 square degrees whose length is five times greater than its width. The first two to have their brightness changed by rolling the third by diving. We consider flashes lasting 0.05 s. For the human eye (with reasonably bright lights) summation is fairly small for areas greater than 1 square degree. We calculate that to produce a threshold increment (five times Barlow's) for the 25 square degree patch would demand a roll of less than 2° and that only a slightly greater roll would be required for the 1 square degree tail spot. Now in steady swimming the tail will roll much more than the body so the small tailspot will produce stronger stimuli than the 25 times larger area on the body. Suppose now that the observer is not one but five fish lengths from the signalling fish. The larger area is now only 1 square degree to the eye of the observer and the smaller one twenty-fifth of a square degree. As summation in the eye is almost complete below 1 square degree the threshold roll for the larger area is only a little greater and still about 2°, an approximately 20° roll would be required of the tail. With respect to the five times one line-shaped patch this would, at one fish length, require a dive of about 4° to reach threshold and a somewhat larger dive at five fish lengths. The sequence of rolling, yawing and perhaps later pitching events in a C-start movement such as that shown in figure 22 must produce massive but meaningful patterns of brightness changes to observers who are many fish lengths distant from the signalling fish but, as we have seen, much smaller movements will produce significant stimuli at distances that would, for example, allow the fish to participate in 'chorus-line' manoeuvres (Potts 1984) whereby 'individuals observe the approaching manoeuvre and time their own execution to coincide with its arrival'. The above analysis can only indicate that the signalling mechanisms described here are likely to be effective at distances which will make them useful to fish. It takes no account of the special properties of the visual systems of fish which evidently are highly specialized, see e.g. the very striking patterns of the receptors described and referred to by Fineran & Nicol (1978) and by Lythgoe (1979), and the estimates of acuity made by Pankhurst (1989). Neither does it take account in our own vision of the visibility of special targets, e.g. lines or gratings (see, for example, Muntz *et al.* 1974).

(*b*) *Comparison with reflections from matt surfaces*

It is instructive to compare the properties of reflecting and diffusing surfaces for camouflage and signalling. Myrberg (1991) has recently published an account, well supported by behavioural data, of the ways in which the markings of sharks e.g. the white tipped 'paddles' of the oceanic whitetip shark, are probably used to transfer information between individuals.

Let us consider the visibility of white and black diffusing (matt) patches on the surface of a fish. By varying the angular setting of such surfaces with respect to the ambient light field, their brightnesses to an observer could certainly be increased or decreased over a wide range of angles of view, and they could, for example, signal rolling or pitching movements. The changes in brightness with angle of roll or pitch would however be much smaller than those given by specular reflectors. Such patches would moreover: (i) not give, as reflective surfaces can, signals which are largely independent of the position of the observer (see figure 6), and (ii) not give the possibility of the fish passing quickly between being almost invisible to sending strong signals to neighbours.

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REFERENCES

Barlow, H.B. 1958 Temporal and spatial summation in human vision at different background intensities. *J. Physiol.* **141**, 337–350.

Denton, E.J. 1970 On the organization of reflecting surfaces in some marine animals. *Phil. Trans. R. Soc. Lond.* B **258**, 285–313.

Denton, E.J. Gilpin-Brown, J.B. & Wright, P.G. 1972 The angular distribution of the light produced by some mesopelagic fish in relation to their camouflage. *Proc. R. Soc. Lond.* B **182**, 145–158.

Denton, E.J., Herring, P.J., Widder, E.A., Latz, M.F. & Case, J.F. 1985 The role of filters in the photophores of oceanic animals and their relation to vision in the oceanic environment. *Proc. R. Soc. Lond.* B **225**, 63–97.

Denton, E.J. & Land, M.F. 1970 Mechanism of reflexion in silvery layers of fish and cephalopods. *Proc. R. Soc. Lond.* A **178**, 43–61.

Denton, E.J. & Nicol, J.A.C. 1965*a* Studies on reflexion of light from silvery surfaces of fish, with special reference to the bleak, *Alburnus alburnus*. *J. mar. Biol. Ass. U.K.* **45**, 683–703.

Denton, E.J. & Nicol, J.A.C. 1965*b* Reflexion of light by external surfaces of the herring, *Clupea harengus*. *J. mar. Biol. Ass. U.K.* **45**, 711–738.

Denton, E.J. & Nicol, J.A.C. 1966 A survey of reflectivity of silvery teleosts. *J. mar. Biol. Ass. U.K.* **46**, 685–722.

Duntley, S.Q. 1963 Light in the sea. *J. opt. Soc. Am.* **53**(2), 214–233.

Fineran, B.A. & Nicol, J.A.C. 1978 Studies on the photoreceptors of *Anchoa mitchilli* and *A. hepsetus* (Engraulidae) with particular reference to the cones. *Phil. Trans. R. Soc. Lond.* B **283**, 25–60.

Franz, V. 1907 Die biologische Bedeutung des Silberglanzer in der Fischaut. *Biol. Zbl.* **27**, 278–285.

Huxley, A.F. 1968 A theoretical treatment of the reflexion of light by multilayer structures. *J. exp. Biol.* **48**, 227–245.

Jannsen, J., Harbison, G.R. & Craddock, J.E. 1986 Hatchetfish hold horizontal attitudes during diagonal descent. *J. mar. Biol. Ass. U.K.* **66**, 825–833.

Jenkin, P.M. 1938 Oxygen production by the diatom *Coscindodiscus excentricius* Ehr. in relation to submarine illumination in the English Channel. *J. mar. biol. Ass. U.K.* **22**, 301–343.

Jerlov, N.G. 1976 *Marine optics*. (231 pages.) Amsterdam: Elsevier.

Jerlov, N.G. & Fukuda, M. 1960 Radiance distribution in the upper layers of the sea. *Tellus* **12**, 348–353.

Kampa, M. 1970 Underwater daylight and moonlight measurements in the eastern North Atlantic. *J. mar. biol. Ass. U.K.* **50**, 397–420.

Land, M.F. 1972 The physics and biology of animal reflectors. *Prog. Phys. Biol.* **24**, 75–106.

Lythgoe, J.N. 1979 *The ecology of vision*. (243 pages.) Oxford: Clarendon Press.

Muntz, W.R.A. Baddeley, A.D. & Lythgoe, J.N. 1974 Visual resolution under water. *Aerospace Med.* **45**(1), 61–66.

Myrberg, A.A. 1991 Distinctive markings of sharks: ethological considerations of visual function. *J. exp. Biol. Suppl.* **5**, 156–166.

Pankhurst, N.W. 1989 The relationship of ocular morphology to feeding modes and activity periods in shallow marine teleosts from New Zealand. *Environ. Biol. Fish.* **26**(3), 201–211.

Partridge, J.C. 1990 The colour sensitivity and vision of fishes. In *Light and life in the sea* (ed. P. J. Herring, A. K. Campbell, M. Whitfield & L. Maddock) pp. 167–184. Cambridge University Press.

Poole, H.H. & Atkins, W.R.G. 1937 The penetration of light into the sea as measured by emission of rectifier photoelectric cells. *Proc. R. Soc. Lond.* B **123**, 153–165.

Potts, W.K. 1984 The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature, Lond.* **309**, 344–345.

Preisendorfer, R.W. 1959 Theoretical proof of the existence of characteristic diffuse light in natural waters. *Contr. Scripps Inst. Oceanogr.* No 1094, 1–9.

Report of the Council of the Marine Biological Association of the UK for 1990. 1991 *J. mar. biol. Ass. U.K.* **71**, 948–949.

Rowe, D.M., Denton, E.J. & Batty, R.S. 1993 Head turning in herring and some other fishes. *Phil. Trans. R. Soc. Lond.* B **338**, 141–148.

Tyler, J.E. 1960 Radiance distribution as a function of depth in an underwater environment. *Bull. Scripps Inst. biol. Res.* **7**, 363–411.

Tyler, J.E. & Smith, R.C. 1970 *Measurements of spectral irradiance underwater*. (103 pages.) New York: Gordon and Breach Science Publishers.

von Holst, E. 1950 Quantitative Messung von Stimmungen im Verhalten der Fische. *Symp. Soc. exp. Biol.* **4**, 143–172.

Ward, F. 1919 *Animal life under water*. (178 pages.) London: Cassell.

Whitney, L.V. 1941 The angular distribution of characteristic daylight in natural waters. *J. mar. Sci.* **1**, 122–152.

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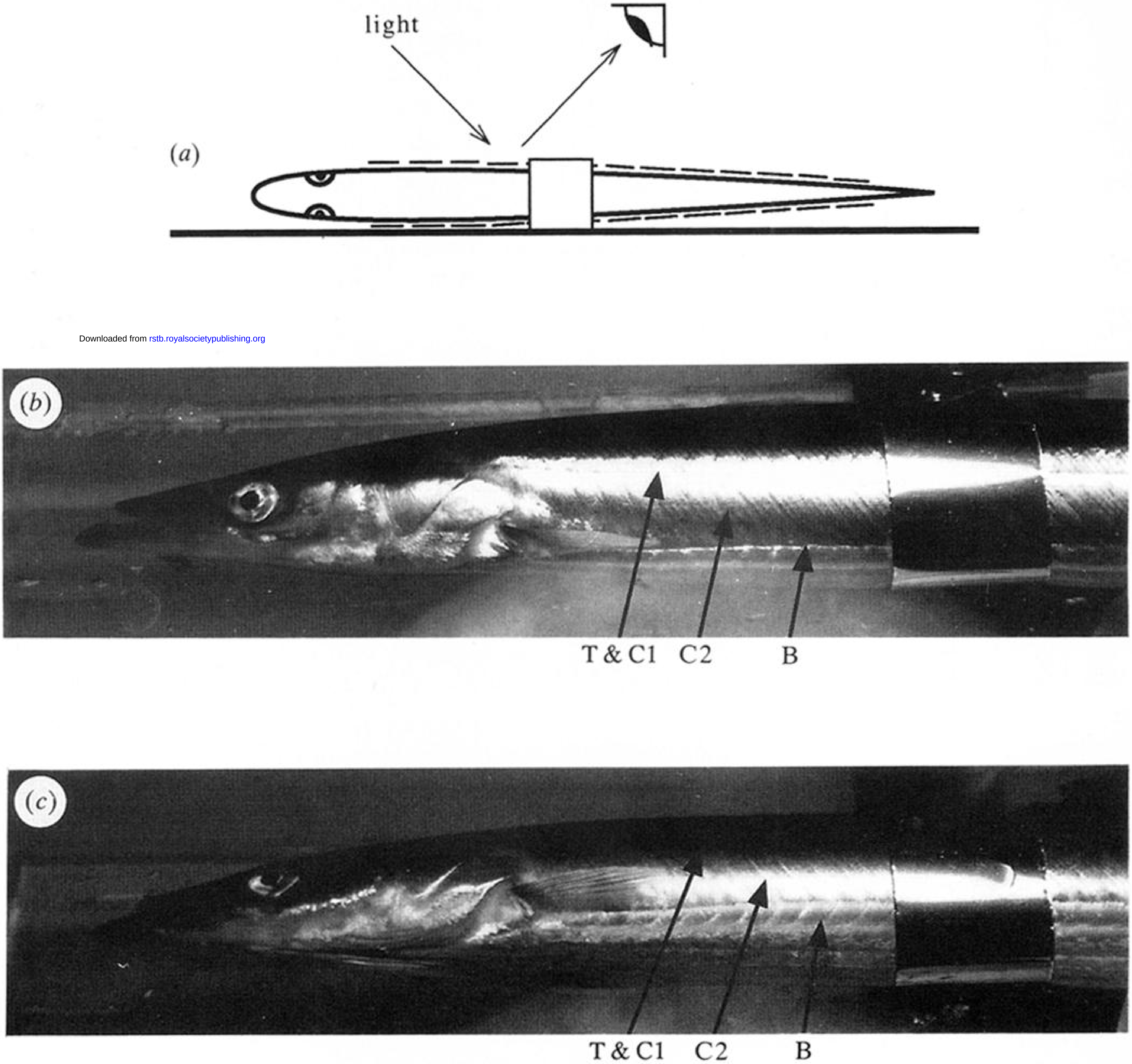
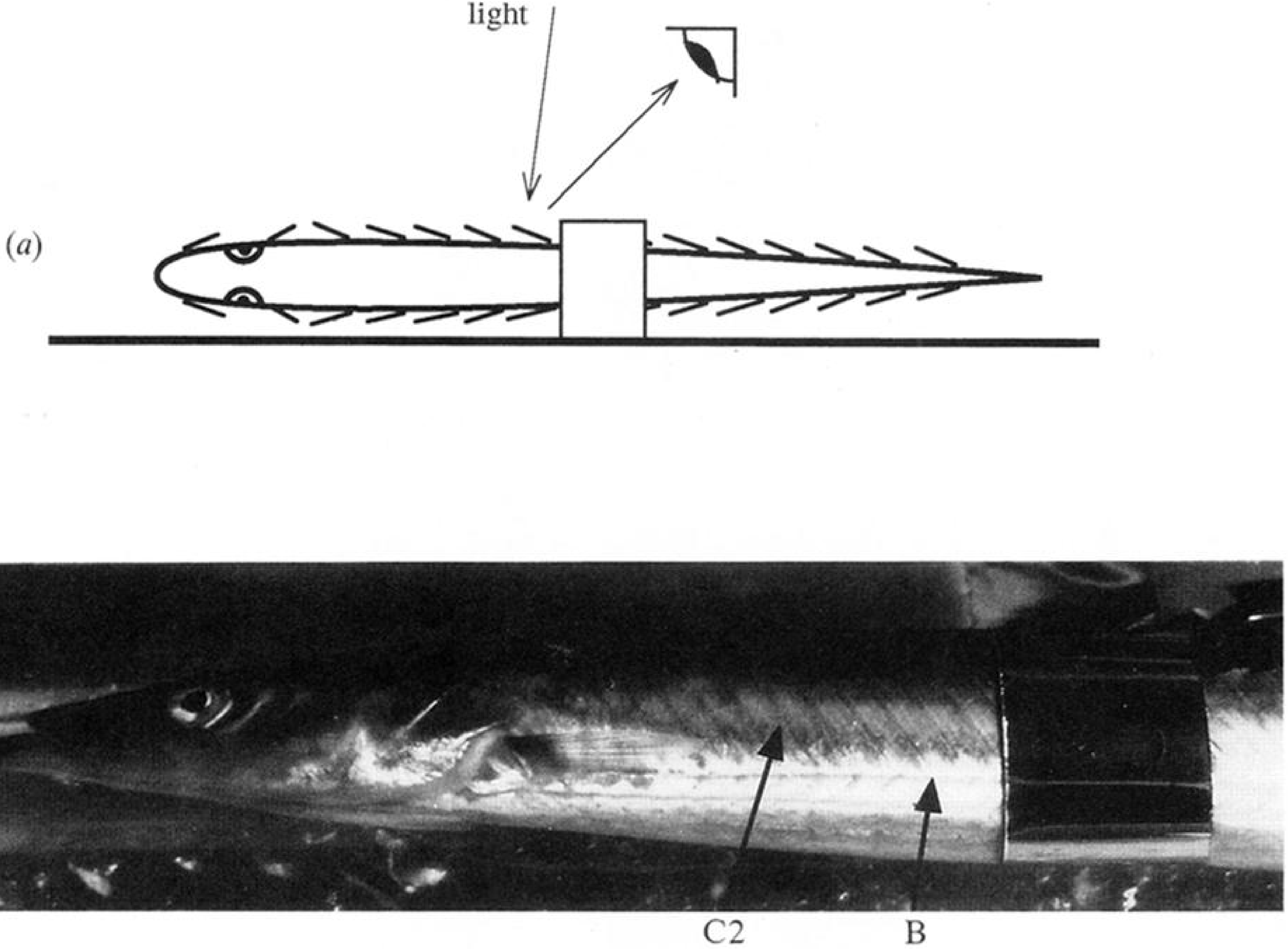
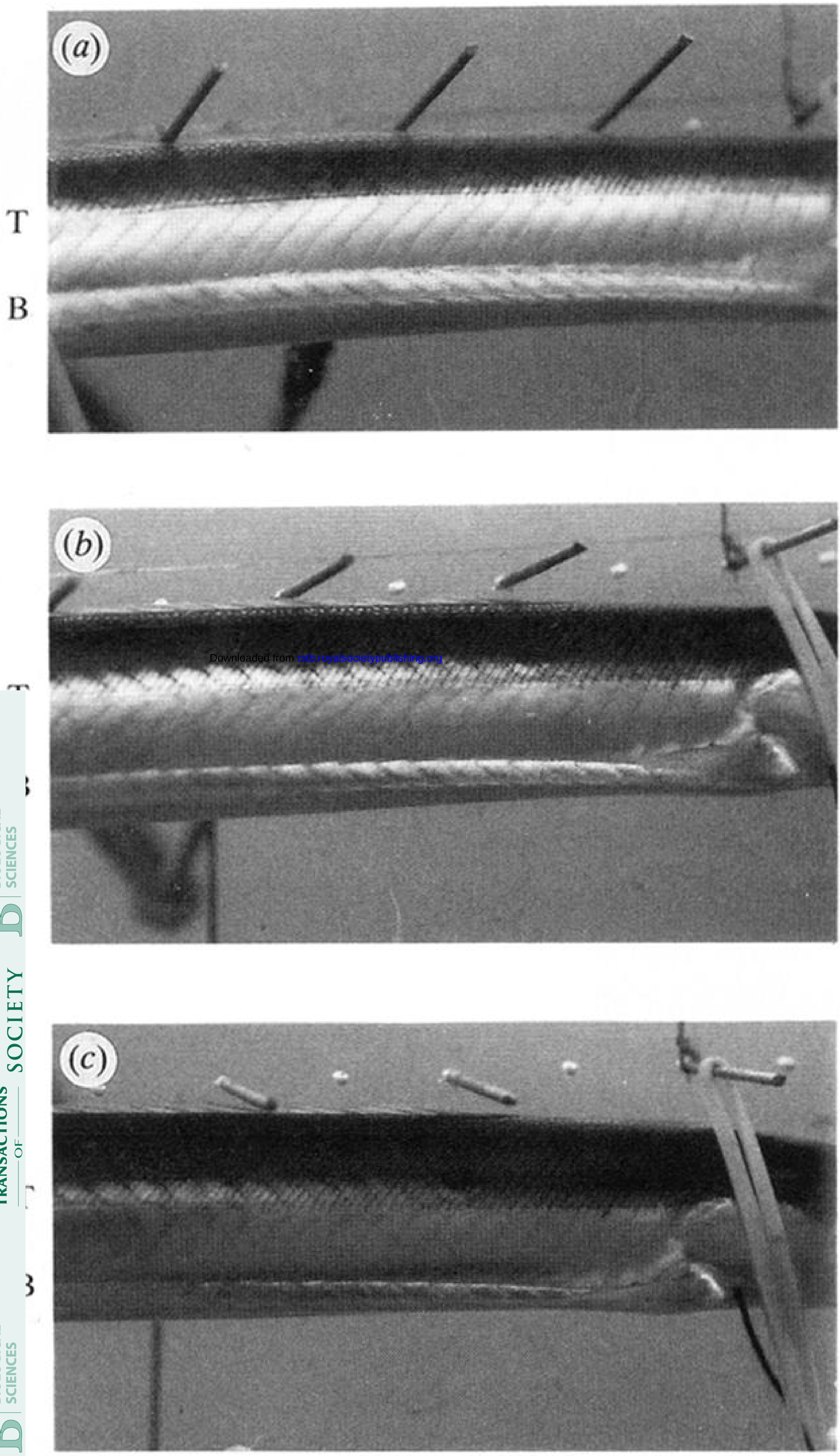


gure 15. (*a*) Diagram of fish lying on a platform which can be rotated around its long axis. The light is inci- nt from the rostral end of the fish, while the fish is viewed from its caudal end. A piece of bright aluminium il has been wrapped around the fish. (*b*) Photograph of a fish; the platform has been rotated to the setting for hich the bands T and C1 gave their brightest reflections. This coincides with the setting for which the adjacent il does so too. (*c*) Similar to (*b*), but the fish has been rotated so that band C2 gave its best reflection: this ain coincided with the best setting for the adjacent foil. Note that the band B stayed dark.

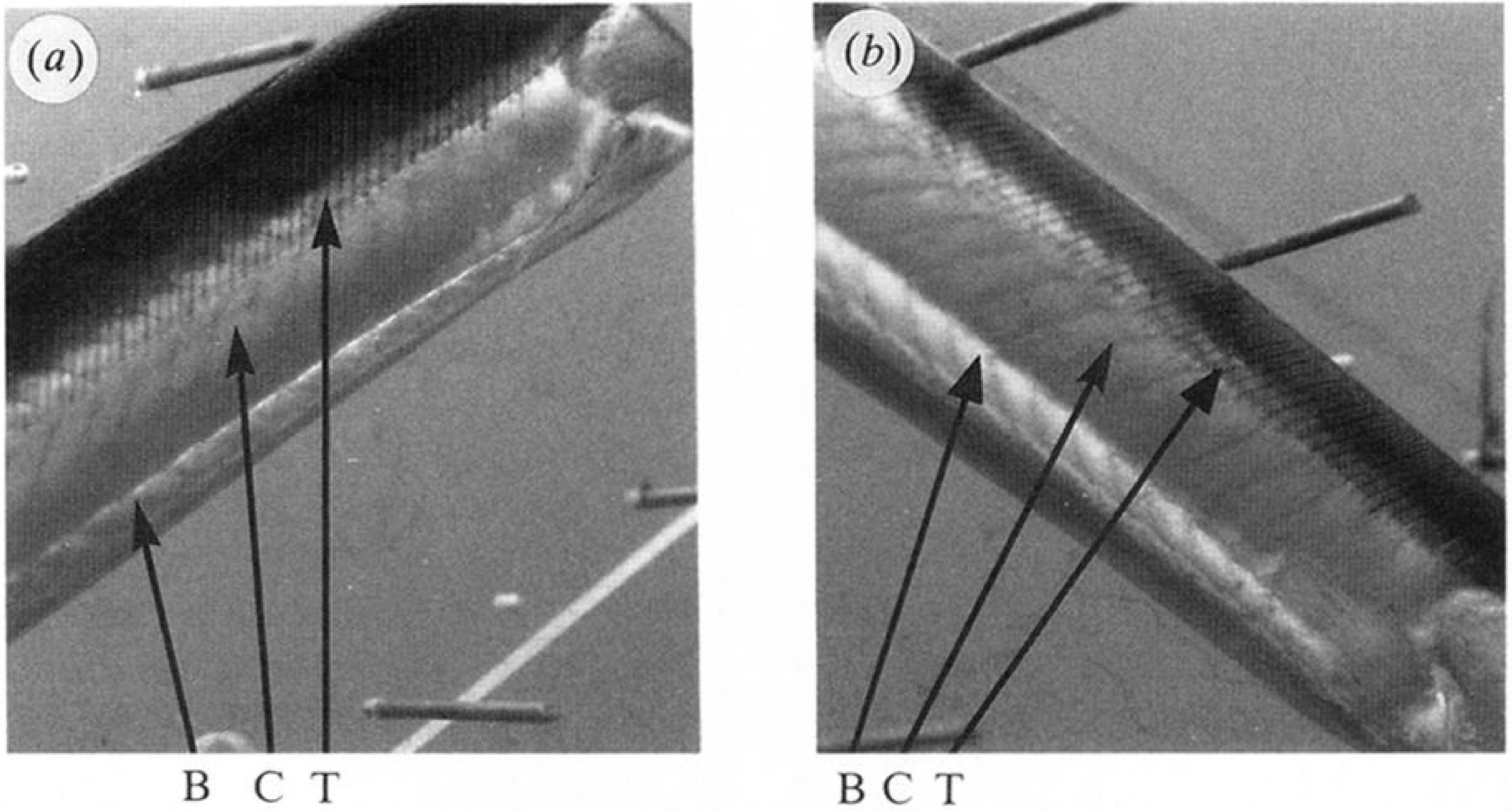


gure 16. Similar to figure 15. To have a bright reflection from the band B of the fish, the directions of the inci- nt light and the point of view have both to be from the caudal end of the fish. This is because the reflecting atelets are tipped towards the tail in band B. The foil now appears dark. Note that at the head end of the fish, e platelets are tipped towards the snout.

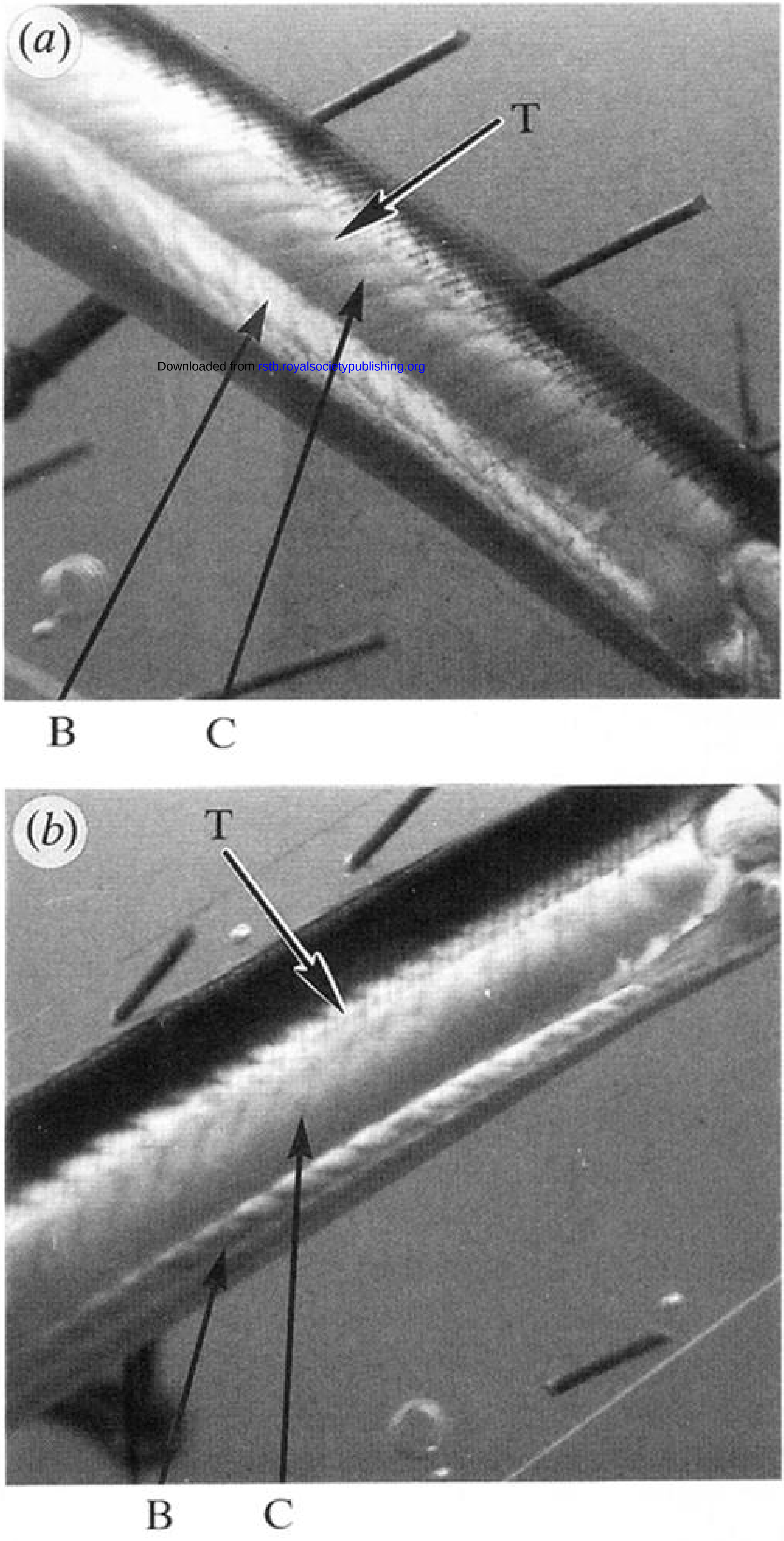
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



gure 17. *Hyperoplus lanceolatus*. Photographs taken in the paratus shown in figure 13 showing the effects of rolling. ie angles of roll are: (*a*) +10°; (*b*) 0°; and (*c*) −10°. The terior end of the fish is to the right-hand side. It can be n that the various bands all become brighter and darker gether. This is a large effect. The brightness of the surface the fish approximately doubles or halves for every 10° of l.



gure 18. Similar to figure 17, but showing the effects of pitching with zero roll. (*a*) Ascending; (*b*) diving. It n be seen that the brightness of bands C and T changes relatively little, whereas the brightness of band B anges a great deal between the fish ascending and diving.



gure 19. Similar to figure 18, but showing the effects of ultaneous pitching and rolling. (*a*) Diving, rolling +10°; ascending, rolling +10°.

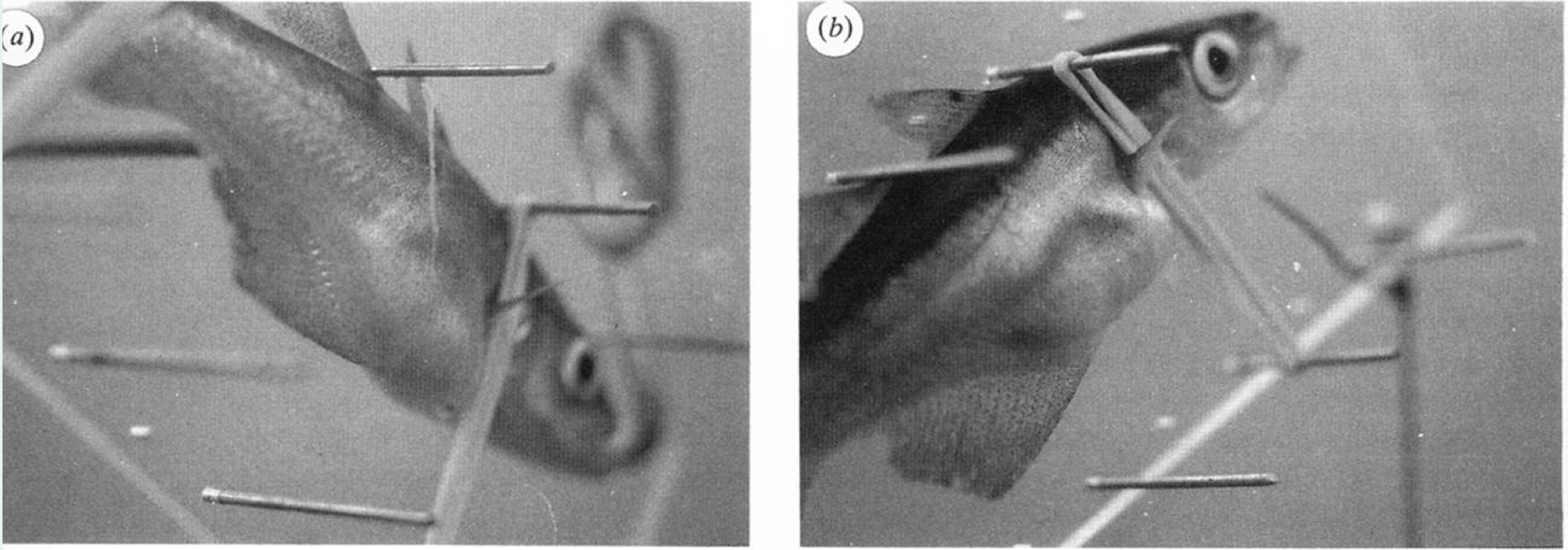
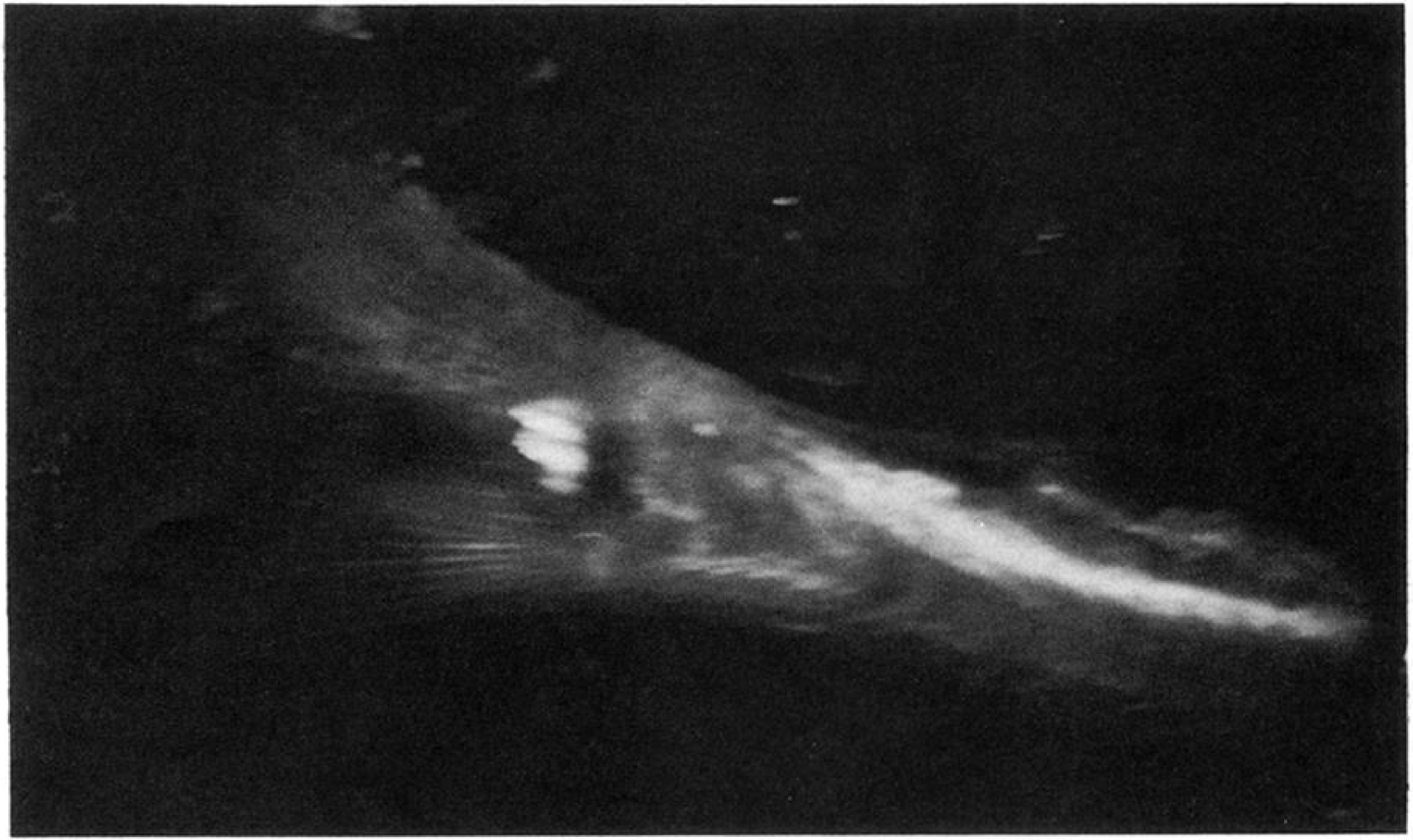
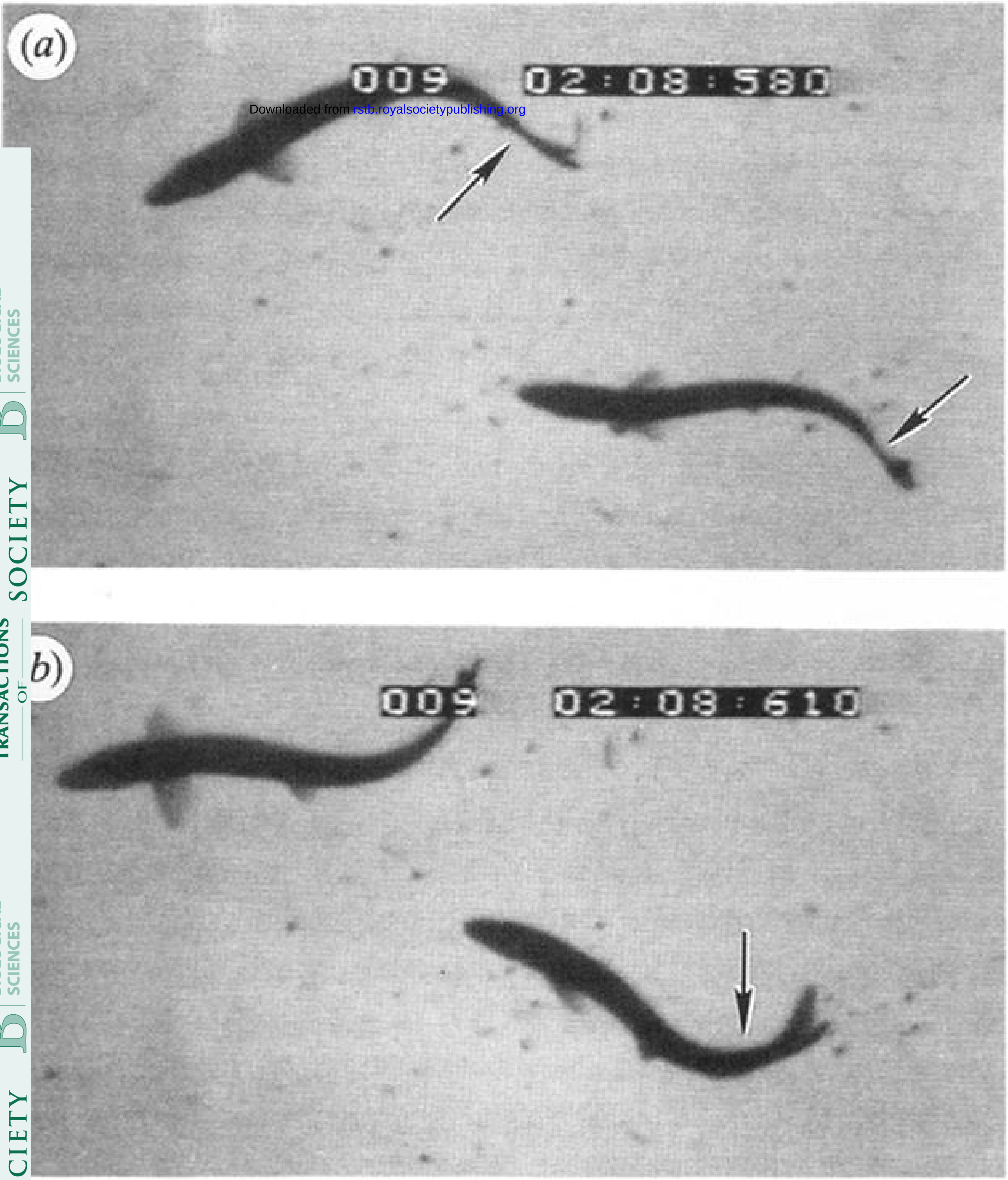


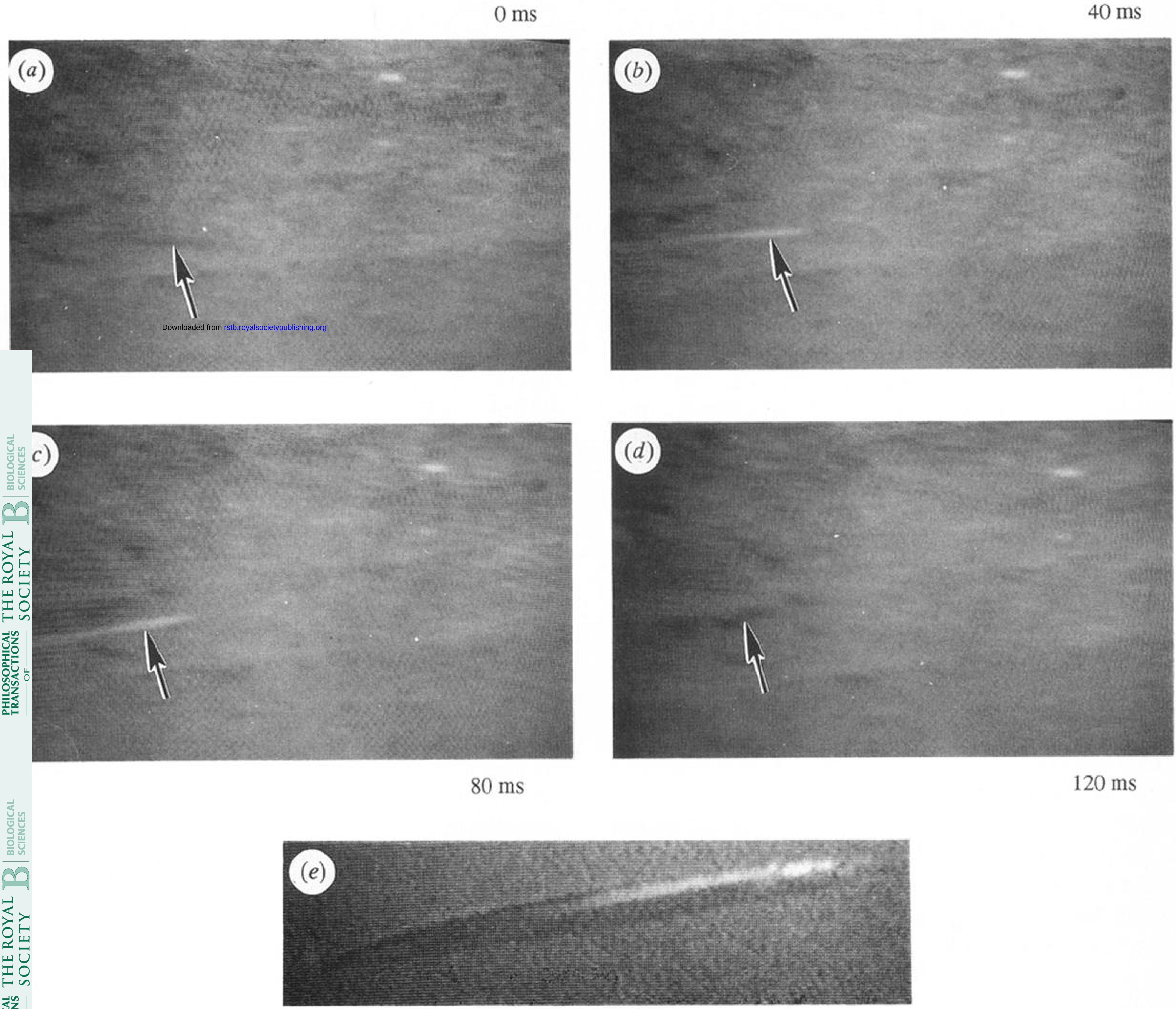
Figure 20. Similar to figure 18 but for a small pollock. (*Pollachius pollachius*). (*a*) Diving; (*b*) ascending. Here, the most striking effect is in the dorsal regions.



gure 21. Photograph of the bright tail-spot of a pilchard (*Clupea pilchardus*); taken in the laboratory.



gure 22. High-speed video-recordings of two herring made the Dunstaffnage Marine Research Laboratory, made by r R. S. Batty. (*a*) the fish are swimming slowly, the caudal duncles (arrowed) are vertical and appears as very thin houettes. (*b*) the lower fish is making a rapid turn and the il has rolled through about 60° in 30 ms.



gure 23. Video recordings made in the sea off Plymouth by Dr G. W. Potts showing a sand eel (*Hyperoplus lan-* *latus*) swimming across the field of view. (*a*–*d*) Four successive frames, 40 ms apart; the fish is very difficult to e on (*a*) and (*d*), but very visible by the light which it reflects on (*b*) and (*c*); (*e*) is a closer view of the fish owing a pattern which depends mainly rolling and ascending.